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MORPHO-PHYSIOLOGICAL FACTORS AFFECTING PLANT PRODUCTIVITY IN BUSH AND VINE FORMS OF WINTER SQUASH (CUCURBITA MAXIMA DUCH)

CYRIL EMERY BRODERICK

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MORPHO-PHYSIOLOGICAL FACTORS AFFECTING PLANT
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(CUCURBITA MAXIMA DUCH.)

University of New Hampshire

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MORPHO-PHYSIOLOGICAL FACTORS AFFECTING
PLANT PRODUCTIVITY IN BUSH AND VINE
FORMS OF WINTER SQUASH (*CUCURBITA MAXIMA* DUCH.)

BY

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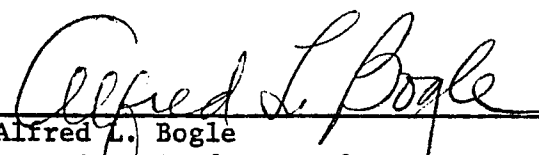
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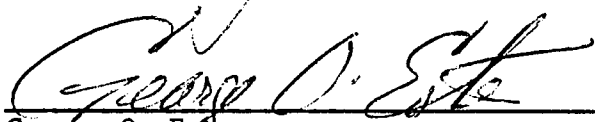
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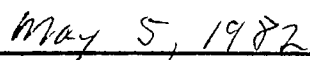
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Date

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This dissertation is dedicated to my wife, Comfort, who has experienced the difficulty of being the wife of a graduate student; to our babies, Cheryl and Cyril, Jr., who had to miss us while they took an extended vacation with their grandparents; and to my parents, Nelson and Sylvia, who have given me every opportunity, every assistance, and their unflinching confidence. With love, this dedication is made to each of you.

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ABSTRACT

MORPHO-PHYSIOLOGICAL FACTORS AFFECTING PRODUCTIVITY IN BUSH AND VINE FORMS OF WINTER SQUASH (Cucurbita maxima Duch.)

by

CYRIL E. BRODERICK

University of New Hampshire, May, 1982

The productivity of a new bush winter squash cultivar ('Autumn Pride') was compared to that of 'Blue Hubbard', a high-yielding vine cultivar. Yields of 'Autumn Pride' increased with increasing plant density and, at high plant densities, were greater than yields of 'Blue Hubbard' at its near optimum plant density.

Several factors could have contributed to the higher yield potential of 'Autumn Pride'. CO_2 compensation points were determined to be 38 ppm and 77 ppm CO_2 for 'Autumn Pride' and 'Blue Hubbard', respectively, at 30°C. 'Autumn Pride' had two layers of palisade parenchyma cells, occupying 74 per cent of the mesophyll. In 'Blue Hubbard' leaves, the second layer of palisade parenchyma was often incompletely formed, so that palisade cells occupied only 52 per cent of its mesophyll thickness. Leaf thickness was not found to be significantly different between 'Autumn Pride' and 'Blue Hubbard'.

Due to its dwarf stem, all 'Autumn Pride' organs were more proximal to their leaves. Furthermore, stems and petioles of 'Autumn Pride' were larger in diameter and contained larger vascular bundles. ^{14}C -sucrose label studies showed that translocation into sink organs over 24 hours

was significantly higher in 'Autumn Pride' than in 'Blue Hubbard'.

Greenhouse and field studies of partitioning showed that total biomass produced by bush ('Autumn Pride') and vine ('Blue Hubbard') plants were equal during the first eight weeks of growth. 'Blue Hubbard' plants partitioned a higher proportion of their dry weight into stems, while 'Autumn Pride' plants had more in leaves and roots. After the eighth week, 'Blue Hubbard' plants became significantly larger than 'Autumn Pride' plants, but 'Autumn Pride' plants had higher harvest indices throughout fruit development. Twelve weeks after transplanting, harvest indices were 70 per cent for 'Autumn Pride' and 57 per cent for 'Blue Hubbard' at low density planting. 'Autumn Pride' plants had a higher specific leaf weight (SLW), a lower leaf area ratio (LAR), and a higher cumulative net assimilation rate (NAR) than those of 'Blue Hubbard'.

I. INTRODUCTION

The high yielding ability of winter squash has been recognized for many years (MacGillivray et al., 1942;1944). Crafts and Lorenz (1944) wrote that "... the cultivated cucurbits ... grow very rapidly, so that the rates noted should represent the upper limits occurring in plants." Whitaker and Davis (1962) were most direct in writing that "Winter squash is exceptional among the cucurbits, and vegetables in general, for its high efficiency in nutrient production."

Despite the productivity of winter squash, it remains a minor crop in most areas of the world. Although a taste preference for squash or squash products must be developed among consumers to stimulate increase in the production of winter squash, a major limitation to the increase in area of production is its vining growth habit. Vines grow randomly and are not easily maintained in small plots or row culture systems. Consequently, cultivation, application of herbicides and pesticides, and other management practices are restricted to their growth and development.

Loomis and Williams (1963) noted that among plants, "Major limiting factors to total seasonal yields appear to be leaf area, its manner of display, and carbon dioxide supply." They recommended that attention to genetic variability in the manner of leaf display may effect crop improvement. Recent improvements of yields of crops such as corn, wheat, cotton, and rice give evidence of the soundness of this advice.

During the last 13 years, a breeding program at UNH has been concerned with the development of high-yielding varieties of winter squash. A recently developed bush strain, named 'Autumn Pride', is characterized

by short internodes and long vertical petioles, resulting in a compact upright form of growth. This strain, which produces large Hubbard-type fruit, lends itself to traditional row crop culture.

Although bush strains are easier to cultivate than vine strains, their ultimate success will depend on their productivity and fruit quality, as compared to vine cultivars. To compare the productivity and efficiency of dry matter production between bush and vine strains, the following objectives were set:

- (1) To determine the yielding ability of the bush strain 'Autumn Pride' at different planting densities, and to compare its general productivity to that of a high yielding vine cultivar.
- (2) To compare patterns of growth and development in bush and vine strains in relation to productivity.
- (3) To identify physiological and morphological attributes of the bush phenotype which may either contribute to or limit productivity in winter squash.

II. LITERATURE REVIEW

Description of Winter Squash

Squash is a name used for several domesticated species of the genus Cucurbita, including cultivars of C. pepo, C. mixta, C. mochata, and C. maxima (Whitaker, 1962). Squash cultivars whose fruits are picked and consumed in an immature condition are known as summer squash. Generally, they have a bush habit of growth and belong to the species of C. pepo. Varieties requiring a 90 to 140-day growing season and whose fruits are harvested at maturity are called winter squash.

Vine-type Winter Squash

Most winter squash cultivars have a vining prostrate growth habit. Internodes of vine cultivars may reach lengths of as much as 16 cm in C. pepo and 22 cm in C. maxima (Denna and Munger, 1962). Vine plants also produce tendrils in leaf axils on stems during their growth. Under field conditions, vine plants produce several secondary and tertiary branches, contributing to rapid growth and extensive leaf canopy development. Adventitious roots form at many nodes in contact with the soil.

Bush-type Winter Squash

The bush phenotype is not frequent in winter squash, but the bush habit is typical of varieties of summer squash. In contrast to vine plants, bush plants are erect, and do not produce tendrils (Whitaker and Davis, 1962). Denna and Munger (1962) reported that bush squash plants appear to differ from vine plants in their general morphology primarily by the length of the individual internodes. They found no difference in the number of internodes in plants grown under field conditions. No

differences in leaf size, thickness of internodes, or size of fruits were reported.

Denna (1963) found that internodes of bush varieties of C. pepo and C. maxima elongated in response to applications of gibberellic acid (GA_3). The total shoot length also increased. At optimal GA_3 levels, bush plants attained growth similar to treated and untreated vine plants. This reversal of the dwarf phenotype of the bush squash plant by GA_3 suggested that the physiological basis of the bush habit was a genetic block in the synthesis of endogenous GA_3 (Denna, 1963).

Singh (1949) evaluated several economic characters of Cucurbita maxima and found the vine habit to have "intermediate" or incomplete dominance over the bush habit. He reported that two genes governed the expression of the bush character. Denna and Munger (1963) reported on the allelism of the bush genes in C. maxima and C. pepo. They concluded that genetic dwarfism in winter squash is a recessive trait based on one gene pair.

The Productivity of Crop Plants

Products of photosynthesis account for more than 90 per cent of the total dry weight of plants, and the mechanism of this process is the primary factor influencing crop productivity. Three photosynthetic processes have been determined to exist among crop plants. They are Calvin cycle (C_3) photosynthesis, Hatch-Slack pathway (C_4) photosynthesis, and Crassulacean Acid Metabolism (CAM) photosynthesis. The product of any of these processes is termed "gross photosynthesis".

"Net photosynthesis" is the typical measure of CO_2 uptake, because there are several subsidiary processes which make it virtually impossible to measure total CO_2 uptake. These processes include both "dark" respi-

ration and photorespiration.

Loomis and Gerakis (1975) summarized numerous studies on the productivity of agricultural crops and concluded that C_4 crops have the highest yield potential. Annual production values illustrated the productivity of C_4 plants. Converted to tons per hectare per day, the C_4 forage, napier grass (Pennisetum purpureum), produced about $0.235 \text{ t ha}^{-1} \text{ d}^{-1}$. Sorghum and sugar cane also produced about $0.225 \text{ t ha}^{-1} \text{ d}^{-1}$. These determinations are confirmed by crop growth rates (CGR's) compiled by Cooper (1975).

Crop growth rate (CGR) is the rate of dry matter production per unit land area. It is expressed usually as the grams of dry matter produced per square meter of ground area per day. Zelitch (1971) wrote that CGR is the most meaningful term for the comparison of species, varieties, or the effect of the environment on productivity. Maximum CGR is about $55 \text{ g m}^{-2} \text{ d}^{-1}$ for C_4 crops and about $40 \text{ g m}^{-2} \text{ d}^{-1}$ for C_3 crops.

Net Photosynthesis and Productivity

The higher crop yields for C_4 plants confirm the predictions of greater efficiency of the Hatch-Slack pathway. Phosphoenol pyruvate carboxylase (PEP_c) effectively traps CO_2 in C_4 acids in mesophyll cells. Each C_4 -acid loses a CO_2 molecule from its structure in bundle sheath cells where the CO_2 molecule is captured and refixed by ribulose-1,5-biphosphate carboxylase in the C_3 compound, 3-phosphoglyceric acid. By this mechanism, the supply of CO_2 to bundle sheath cells is a sink of metabolic energy since C_4 metabolism uses an extra mole of ATP per mole of C_4 -acid synthesized. For maximum efficiency in the C_4 pathway, therefore, the ATP supply must be non-limiting. This is the case in high light intensity environments where the light reaction of photosynthesis

produces large amounts of ATP for use in the enzymatic (dark) reactions.

In light-limiting environments, C_4 plants lose their advantage due to inadequate synthesis of ATP. They perform as well as or poorer than C_3 plants in these environments. This consideration is why C_4 plants are most productive at lower latitudes (Loomis and Gerakis, 1975).

PEP_c is virtually absent in C_3 species. Where present, PEP_c levels are low. C_3 species rely on the enzyme $RuBP_{c/o}$ to carry on photosynthesis. The fact that $RuBP_{c/o}$ is both a carboxylase and an oxygenase makes competitive inhibition of photosynthesis by O_2 an important feature of C_3 plants.

C_3 plants may also yield quite well despite the inefficient supply of carbon dioxide. C_3 metabolism is typical of most crop plants, and yields are good under most conditions. There are examples of C_3 plants attaining yields comparable to those of C_4 plants. Zelitch (1971) mentioned sunflower and cattail as species which may be very efficient for reasons not associated with C_4 metabolism.

Net photosynthetic rates of 50 to 85 mg CO_2 per square decimeter of leaf per hour have been obtained for C_4 plants (Zelitch, 1971). Typical values for C_3 plants range between 10 and 50 mg CO_2 per square decimeter of C_3 plant leaf (Zelitch, 1971). These values illustrate the large range for C_3 plants, and they accentuate the higher rates for C_4 plants.

Gifford (1974) pointed out that there is no apparent difference in productivity between the best examples of C_3 and C_4 plants growing in their preferred environments. This environment-dependent factor was also recognized by Kelly et al. (1976) in their discussion of C_3 and C_4 metabolism. Consequently, highly productive species of both C_3 and C_4 metabolism coexist in the agricultural world.

The importance of Crassulacean Acid Metabolism (CAM) is also recognized. CAM plants such as Ananas comosus (pineapple) utilize the same enzymes and substrates as those of C_4 plants.

Photorespiration and Productivity

Respiration is the difference between gross photosynthesis and net photosynthesis. It is the oxidation of foods in living cells with the resultant release of energy (Meyer et al., 1973). Both aerobic and anaerobic respiration occur in plants and are referred to as "dark respiration", as contrasted to photorespiration.

Photorespiration is a light-dependent release of CO_2 believed to be associated with the metabolism of glycolate (Zelitch, 1971; Kelly et al., 1976). Numerous studies show that atmospheric oxygen interacts in C_3 photosynthesis by an O_2 and light-stimulated formation of glycolate and the subsequent oxidation of glycolate to CO_2 , and by the direct inhibition of photosynthesis by oxygen (Warburg effect) (Chollet and Ogren, 1975).

High photorespiratory rates reduce net photosynthesis, and the lower photosynthetic rates of C_3 plants have been linked to the activity on RuBP by an oxygenase. In atmospheres low in oxygen or high in carbon dioxide, it has been shown that photosynthesis can be as efficient in C_3 species as in C_4 species. Zelitch (1979) discussed the improbability of raising the CO_2 level in the open environment, but he mentioned its use in the greenhouse.

Although photorespiration can significantly reduce net photosynthesis, there have been suggestions that under certain environmental conditions, photorespiration may be a protective mechanism in photosynthesis,

essential for undisturbed growth, or even survival, of plants (Heber and Krause, 1980).

CO₂ Compensation Point and Productivity

The CO₂ compensation point is that CO₂ level at constant light intensities above the light compensation point at which there is no net CO₂ exchange between the plant and its environment (Zelitch, 1971). Numerous results show that CO₂ compensation points range between 30 and 100 ppm for C₃ plants, and less than 10 ppm for C₄ plants (Zelitch, 1971; Larcher, 1980). This emphasizes that C₄ plants can exploit lower concentrations of atmospheric CO₂ while efficiently carrying out photosynthesis. Thus, the CO₂ compensation point can be used to distinguish between C₃ and C₄ plants.

Because of the wide variation in carbon dioxide compensation points among C₃ plants, it is frequently assumed that measurements of the CO₂ compensation point among varieties of a crop may lead to the selection of varieties with higher photosynthetic rates. Moss et al. (1969) measured compensation points of 100 genetic lines of wheat and 20 lines of barley and detected no differences in CO₂ compensation points among the varieties of wheat or barley.

In an evaluation of CO₂ compensation points of 44 soybean genotypes, Cannell et al. (1969) found one soybean genotype with a slightly higher CO₂ compensation point. Both of these experiments were based on the longer survival in a closed system of the varieties with lower CO₂ compensation points. Zelitch (1971) noted that the fairly constant CO₂ compensation points found among the varieties showed that if differences in photorespiration and CO₂ compensation points occur, the method of assay may be the most determining factor in distinguishing differences

in compensation points.

Procedures for evaluating compensation points with adequate replications of genotypes are limited. The infra-red gas analyzer (IRGA) is a good instrument for photosynthetic measurement, but its high purchase price, maintenance costs, long assay period, and long periods of adjustment between assays hinder its use in making large numbers of photosynthetic measurements.

Ross (1974) presented a rapid technique by which CO_2 compensation points for plant leaves can be determined by measuring changes in pH of a bicarbonate solution in a closed atmosphere (flasks or glass bottles) containing the leaf of the genotype in question partially inserted in a vial of water.

Plant Anatomy and Productivity

Kranz anatomy is a physiological term now used to describe the anatomy of most C_4 species. Kranz, a German word meaning "wreath-like", describes the mesophyll and bundle sheath whorl of cells surrounding vascular bundles in leaves high in PEP_c and known to be carrying on C_4 metabolism (Brown, 1958; Laetsch, 1974; Essau, 1977). Metcalfe and Chalk (1979) listed the families and genera in which Kranz anatomy has been found. Today, about a thousand C_4 plant species are known (Black, 1976). No species of the Cucurbitaceae has been found to exhibit C_4 characteristics of C_4 metabolism. Ting and Kluge (1980) listed one member of the Cucurbitaceae as a CAM plant.

On the origin of Kranz anatomy, Metcalfe and Chalk (1979) quoted Moser who in 1924 wrote that Kranz anatomy may be the climax of development from isobilateral leaf arrangements in plants.

Other leaf characteristics affect photosynthesis. Zelitch (1971)

noted that as leaf thickness increases, CO_2 assimilation would increase if more chloroplasts and a larger cell surface were exposed to CO_2 without accompanying increases in respiration and path length. The presence of chloroplasts in abundant numbers on both the adaxial and abaxial surfaces affect leaf photosynthetic rates. Nobel (1974) discussed the effect of leaf thickness on photosynthesis. He mentioned that xerophytes tend to have a somewhat more highly developed palisade region than do mesophytes, and that sun leaves usually have a higher proportion of palisade cells than shade leaves on the same plant. He also stated that palisade cells are generally longer in sun leaves than in shade leaves. Another factor is the proximity of vascular tissues to assimilating tissues (Metcalf and Chalk, 1979). Wardlaw (1980) discussed the advantage conferred in vein-loading by the proximity of C_4 photosynthesizing cells to vascular bundles.

Translocation and Productivity

Rates of translocation have been reviewed by Canny (1973). There are large variations in rates within and among species. The use of radioactive tracers is the typical mode for the evaluation of translocation rates. Canny (1973) noted that non-destructive sampling methods using replicates of uniform plants also yield precise data.

Rates of transport of assimilates out of leaves of Cucurbita melopepo were measured by Webb and Gorham (1964). They recorded a minimum velocity of 290 cm hr^{-1} . In Cucurbita pepo, Webb and Burley (1964) obtained a rate of 28 cm hr^{-1} . Webb and Gorham (1965) explained some of this variation in terms of variation in tissue age, and attributed the largest values to longitudinal transport. These values compare with 87 to 109 cm hr^{-1} in Triticum stems (Wardlaw, 1965), 42 to 150 cm hr^{-1} in

Saccharum (Hart et al., 1963), 50 to 135 cm hr⁻¹ in Beta (Mortimer, 1965) and 60 cm hr⁻¹ in Helianthus (Lee et al., 1966). Evans and Wardlaw (1976) reported that C₄ grasses have very high rates of translocation.

Mass transfer measurements may be more appropriate in comparing translocation within or among species. Specific mass transfer (SMT) is a term coined by Canny (1973, 1975) to compare translocation efficiencies, considering phloem area among different species. Values for the feeding of fruit sinks were 4.5 to 4.8 g hr⁻¹ per cm² of phloem for Cucurbita (Cowell, 1942; Crafts and Lorenz, 1944), 4.5 for Solanum (Dixon and Ball, 1922), 4.4 for Triticum (Evans et al., 1970), and 4.2 for Dioscorea (Maron and Lewen, 1926). SMT measured in petioles of Helianthus annuus by Sachs (1884) gave values of 4.6 g hr⁻¹ cm⁻² phloem (Canny, 1975). These values represent maximal rates of mass transfer in C₃ species.

Hofstra and Nelson (1969) found that C₄ plants export at a higher rate than C₃ plants. Lush and Evans (1974) demonstrated that C₄ gramineae maintain SMT rates 3 to 4 times higher than those found in C₃ grass leaves. Part of this efficiency, they argued, was due to the proximity of loading zones to transport tissues. They noted that the distance traversed from the site of fixation in C₃ species to the phloem is 2 or more times that of C₄ species. Evans and Wardlaw (1976) cited additional references to emphasize this limitation of C₃ gramineae.

Translocation from Source Leaves

The Münch hypothesis of 1930 states that water enters the sieve tubes to counteract the build-up of solutes. Osmotic pressure develops with the intake of water. This pressure becomes the driving mechanism of phloem transport. This is the most successful hypothesis to date (Milburn, 1975). The magnitude of this osmotic pressure will depend on

the supply of solutes. This supply depends on phloem loading, and phloem loading depends on the magnitude of photosynthesis. This is the most determining consideration to transport rates and mass transfer, both of which are increasingly being studied.

Using ^{14}C -sucrose, Adedipe (1975) showed that more than fifty per cent of the fed activity was retained in the leaves of Hibiscus esculentus 24 hours after the leaf was fed. He also found that high levels of N and P enhanced the export of ^{14}C .

Edmeades et al. (1979), using $^{14}\text{CO}_2$ in maize, found that as plant density increased, so did the proportion of labelled assimilates remaining in leaves. Ryle et al. (1981) showed that doubling of light intensity also doubled the export of labelled assimilates from the fed leaf to the stolons of white clover. Vicia faba leaves fed with $^{14}\text{CO}_2$ retained substantial amounts of radiocarbon which was initially fixed (Ismail and Sagar, 1981).

One further note about the translocation out of leaves is the discovery that stachyose is the major carbohydrate transported in squash (Webb and Burley, 1964; Webb and Gorham, 1964, 1965; Hendrix, 1977). The question remains whether the transport of this raffinose family polymer is of specific significance in the efficiency of translocation. In addition, it is puzzling that in phloem exudates from species of the Cucurbitaceae, carbohydrates are quantitatively only a minor constituent, reaching no more than one per cent of the exudate by fresh weight; nitrogen compounds were found to be predominant (Crafts and Lorenz, 1944; Zeigler, 1971). The exceptionally high content of nitrogenous substances in the phloem of Cucurbita species (Zeigler, 1975) may be one of the essential features which account for the high rates of translocation rates

in squash. Nitrogen has been reported to affect the translocation and distribution of various substances in plants (Murata, 1969); its role in the physiology of Cucurbita maxima may be very prominent in the efficiency of growth and development in this species.

Translocation into Vegetative Tissues

The sinks during vegetative growth are the shoot and the root, and the plant must channel assimilates into establishing leaf area and root distribution. Different plants have adapted different strategies, and comparative vegetative shoot and root development determine the effectiveness of the development of the sink tissue of economic interest.

Typical vegetative tissues have minimal storage capacity. As sinks, they assimilate cellulose, lignin, chlorophyll, proteins and other complex products of metabolism. Because of the complexity of these substances, there is a tremendous quantity of energy used to convert the sugars, which are the primary products of photosynthesis, into these molecules (Penning de Vries, 1975). The relatively small size of vegetative tissues is a second major limitation to transport to vegetative sinks.

Ryle et al. (1981) found that more than 50 per cent of the ^{14}C assimilated by white clover remained in the source leaf 24 to 48 hours after feeding. In the case of red clover, they found only 23.4 and 18.0 per cent, respectively, remaining in the leaf at 24 hours and 48 hours after feeding. It is interesting to note that white clover forms adventitious roots on stolons; red clover does not form stolons or adventitious roots (Ryle et al., 1981). Plant morphology may play a significant role in the translocation of assimilates into various vegetative organs.

Translocation into Fruit Sinks

In contrast to vegetative tissues, fruit sinks are large, and carbohydrates form a large portion of the intake of fruit sinks. It is reasonable to assume, consequently, that the feeding of fruit sinks can account for significant amounts of translocation out of source leaves.

The mechanism of inhibition of photosynthesis by the accumulation of end products of the photosynthetic process (Neales and Incoll, 1968) is now a corollary to evidence that sinks may stimulate photosynthesis (Geiger, 1976). Kiesselbach (1948) found that crop dry weight was decreased 27 per cent with the removal of corn ears at silking. King et al. (1967) recorded a 40 per cent decline in flag leaf photosynthesis within one day after ear removal. Flinn (1974) found a positive correlation between growth rates and photosynthetic rates of peas. Crews et al. (1975) obtained similar correlations between peach growth and photosynthesis. Setter et al. (1980) showed that the removal of pods from soybean plants greatly reduced leaf photosynthesis. These results indicate the strong effects of sink demand on photosynthesis and productivity.

Plant Environment and Crop Productivity

Blackman and Black (1959) pointed out that with today's knowledge of photosynthesis, maximum productivity can be calculated from energy inputs. Loomis and Gerakis (1975) estimated that C_3 plants convert at least 3 to 4 per cent of incoming light energy into dry matter, and that C_4 plants convert at least 5 to 6 per cent of incoming light into dry weight. Although the above values underscore the efficiency of C_4 plants, Loomis and Gerakis (1975) emphasized the contribution of environmental factors to yield. In general, C_4 plants significantly outyield C_3 plants at low latitudes, are equal to C_3 plants at intermediate lati-

tudes, but are inferior to C_3 plants at higher latitudes.

The productivity of crop plants also depends on the growth period, i.e., the number of days to harvest. Cooper (1975) compared the productivity of different crops in different environments using actual yield data published by numerous independent researchers. Temperate forage yields averaged 22 t ha^{-1} ; tropical forages averaged 64 t ha^{-1} and subtropical forages averaged 34 t ha^{-1} . Tropical and subtropical forages grow throughout the year, whereas temperate forages undergo cyclic growth due to the winter season and thus exhibit lower yields. The yield of tropical forages is greater than that of subtropical forages primarily because most tropical grasses are C_4 species.

Average biological yields of tuber crops were 26 t ha^{-1} , 30 t ha^{-1} , and 32 t ha^{-1} , respectively, for temperate, tropical and subtropical environments. The average biological yields of cereal crops were 21 t ha^{-1} for temperate and tropical and 31 t ha^{-1} for subtropical regions. Subtropical regions receive more insolation due to less cloud cover than the low tropics.

Economic yields of temperate crops averaged 18 t ha^{-1} for forages, 12 t ha^{-1} for tubers and roots, and 8 t ha^{-1} for cereal grains. For tropical crops, the average was 64 t ha^{-1} for forages, 17 t ha^{-1} for roots and tubers and 10 t ha^{-1} for cereals.

As expected, forage crops produced the highest yields. Their photosynthetic organs constitute the yield, and they do not undergo extra metabolic costs in storing photosynthates in complex sink organs. Root and tuber sinks undergo intermediate metabolic costs, and fruit (including grains) sinks undergo high metabolic costs.

The Productivity of Winter Squash

Evaluating the productivity of vegetable crops on the basis of actual food constituents, MacGillivray et al. (1942, 1944) ranked winter squash with potatoes and several other crops as the most efficient nutrient producers. The question is now raised, though, about how winter squash would compare with corn, sugar cane, wheat, sunflower, and other non-vegetable crop plants in terms of productivity.

Cummings and Stone (1921) evaluated the yielding ability and fertilizer response of 'Blue Hubbard' grown in Vermont: Fresh weight yields around $35,927 \text{ kg ha}^{-1}$ were obtained at 2.4 m by 2.4 m spacing, and with two plants per hill in fertilizer trials. Hepler (1941) obtained yields between $29,191 \text{ kg ha}^{-1}$ and $35,927 \text{ kg ha}^{-1}$ at the New Hampshire Agricultural Experimental Station. Although yields obtained by the above researchers are low by today's standards, they recognized 'Blue Hubbard' as one of the highest yielding winter squash cultivars. No data on the yield of bush plants have been found.

Hutchins and Croston (1941) compared the productivity of several cultivars of C. maxima and the F_1 hybrids. 'Mammoth Chili' produced the highest fresh weight fruit yield of $54,029 \text{ kg ha}^{-1}$; 'Kitchenette' yielded $31,052 \text{ kg ha}^{-1}$, 'Banana' yielded $21,957 \text{ kg ha}^{-1}$, and 'Blue Hubbard' yielded $18,231 \text{ kg ha}^{-1}$, all at 2.7 x 2.7 m spacing. Fresh weight biological yields averaged around $60,413 \text{ kg ha}^{-1}$ for 'Mammoth Chili', 'Kitchenette', 'Banana' and 'Blue Hubbard'. Dry weight yields were not determined in these trials.

Plant Density and Productivity

Plant Density

The quantitative relationship between plant population and plant yield has been under continuous study in crop plants. Holliday (1960)

reported that there are two yield responses to increasing plant density. An asymptotic response is where yield increases and is then maintained at a maximum with increasing plant density. The parabolic response is the increase in yield with increasing plant density to a maximum yield followed by a decline in plant yields at higher plant densities.

Asymptotic responses are typical of forages and other crops grown for their vegetative portions, whereas, grain yield generally conforms with a parabolic relationship. Willey and Heath (1969) recognized that for many crops which show an asymptotic response, grading of the economic product may essentially transform the asymptotic yield response to a parabolic one. By grading, small and poor quality harvested products are discarded, thereby often reducing yields appreciably in high density populations.

Several plant densities have been recommended for good winter squash yields. Oyer and Sheldrake (1963) recommended 1.8 to 2.4 m between rows and 0.6 to 0.9 m between plants in row for growing vine crops of winter squash in New York State. Lorenz and Maynard (1980) recommended 0.9 to 1.5 m between rows and 0.6 to 1.2 m between plants in row for bush plants of summer squash, and 1.8 to 2.4 m between rows and 0.9 to 2.4 m between plants in row for vine plants. These spacing recommendations represent plant densities between 1736 and 9260 vine plants per hectare and between 5556 and 18,519 bush plants per hectare. Maximum yields of 'Buttercup' and 'Blue Hubbard' cultivars of C. maxima have been obtained at densities of 3000 to 4500 plants per hectare (Loy, personal communication).

Patterns of Spacing

Patterns of spacing, direction of rows, distance between plants, and distance between rows are all intrinsic to the effect of plant density on yield. Willey and Heath (1969) noted that in describing the relationship

between plant population and crop yield, the effects of spatial arrangements (retangularity) as well as those of plant density are important. Shibles et al. (1975) noted that although soybeans, for example, are grown in rows 75 to 100 cm wide, 30 to 50 cm rows give substantially greater yields. Duncan (1969) stressed the necessity for increased uniformity of plants for the high planting rates necessary for higher yields. He stated that hexagonal plant spacing is mathematically the best planting pattern, and that multiple seeds per hill are the worst.

Production and Partitioning of Plant Biomass

The product of photosynthesis over time is not equivalent to total plant biomass. Penning de Vries (1975) noted that plant biomass is a complex accumulation of primary and secondary products of photosynthesis, such as proteins, carbohydrates, lipids, lignin, and other biochemical components. A proportion of "net photosynthesis" is utilized by plant tissues and organs in the synthesis of these complex constituents, the true assimilates.

Partitioning is the manner in which dry matter becomes part of different tissues and organs of the plant (Wareing and Patrick, 1976). There are definite patterns of growth, where partitioning is between the shoot and root, effecting a shoot-root balance which varies among varieties, and among environments. Then there is the period of storage, where there is accumulation of assimilates within one specific plant part. This plant part may be a tuber such as potato, a root as sugar beet, a stem as sugar cane, leaves as cabbage, or reproductive organs, such as fruits of apple or squash, and grains of cereal crops (Wardlaw, 1968; Evans, 1972; Good and Bell, 1980). The earlier exponential growth followed by storage contrasts strongly with the condition of constant partitioning between growth and storage (Wareing and Phillips, 1970; 1978).

Leaf Growth and Development

Leaves are the primary, although not the sole, photosynthesizing organs. Leaf photosynthesis usually accounts for 90 to 95 per cent of the accumulated plant biomass.

The vegetative phase of partitioning between shoot and root is of fundamental importance. Maximum dry matter production depends on the reinvestment of as high a proportion of assimilates as possible into leaf tissue (Wareing and Patrick, 1975). Expenditure into stems, petioles, and roots should be no more than that which is required to adequately supply mineral nutrients and water (Watson, 1971) and to maintain plant structure.

Wareing and Patrick (1975) noted that "the overall utilization of assimilates in leaf production will depend upon: (1) the rate of new leaf initiation; (2) the rate of leaf growth and final leaf size, and (3) the branching habit, i.e., the number of active shoot apices."

Leaf Area Index: To describe leaf area in terms of land occupied by a plant population, Watson (1947) introduced the term leaf area index (LAI). LAI is defined as the ratio of total area (m^2) of plant leaves per square meter of land [$LAI = (m^2 \text{ of plant leaf}) / (m^2 \text{ of land})$]. LAI varies among species, and even among varieties within a species at similar planting densities (Watson, 1952).

The optimal LAI for a crop depends on plant height and seasonal light intensity, and also varies with size, shape, and angle of leaves (Loomis and Williams, 1969). Optimal LAI for rice has been determined to be between 4 and 8 (Chandler, 1969; Yoshida, 1972). Zelitch (1971) cited reports of LAI's between 4 and 8 for wheat, alfalfa, and clover. Edmeades and Daynard (1979) found that LAI's between 4.0 and 9.0 pro-

duced the best yields in corn. Shibles and Weber (1965) found that the optimal LAI for soybeans was about 4.0. According to Cock et al. (1979), the optimal LAI for cassava varied between 3.0 and 4.0.

Leaf Area Duration: Watson (1947) also introduced the term leaf area duration (LAD). Leaf area duration is "a measure of the ability of the plant to produce and maintain leaf area, and hence its whole opportunity for assimilation" during a growing season (Watson, 1947). Whereas LAI is an index at a particular time in the growth of a crop, LAD integrates the leaf area index over an entire growing season. To afford comparison among species, varieties or strains of different growth duration, LAD is reduced to a weekly statistic (LAI week^{-1}).

Leaf Area Ratio and Leaf Weight Ratio: The ratio of total leaf area to total plant mass is termed the leaf area ratio ($\text{LAR} = \text{dm}^2 \text{ mg}^{-1}$). It is an indication of the effectiveness of dry weight production per unit area (Wallace et al., 1972). The ratio of total leaf weight to total plant weight is the leaf weight ratio ($\text{LWR} = \text{g leaf g}^{-1} \text{ plant}$). These statistics are important in the analysis of the partitioning of dry weight.

Specific Leaf Weight: Specific leaf weight (SLW) is the leaf dry weight per unit leaf area ($\text{SLW} = \text{mg leaf cm}^{-2} \text{ leaf area}$). Although assimilate content in leaves varies and may alter this relationship, Wallace et al. (1972) noted that SLW largely reflects leaf thickness, and they cited several reports where strong positive correlations were obtained between specific leaf weight and net assimilation rate, leaf nitrogen content, and net carbon exchange (NCE) rate. They noted that the correlation held when specific leaf weight (SLW) was altered by variation in light intensity. Wallace et al. (1972)

also cited several studies in which no correlation was found between SLW and leaf thickness. Wilson and Cooper (1969) reported that SLW cannot be considered an estimate of net exchange rate.

Net Assimilation Rate: Net assimilation rate (NAR) is the rate of increase in dry weight per unit leaf area [$\text{NAR} = (1/\text{LAI})(dW/dt)$]. It is a term developed by R. Gregory in 1917 (Watson, 1952), and is equivalent to the amount of dry weight synthesized by one square meter of leaf per day ($\text{NAR} = \text{g dry weight m}^{-2} \text{ of leaf area day}^{-1}$). NAR measures variation in the rate of photosynthesis, but because it cannot account for losses by respiration, it is simply an estimate of net photosynthetic ability among plants. Zelitch (1971) cited several reports which showed large variations in NAR among crop plant environments. He also noted several reports in which close correlations have been found between NAR and total solar radiation.

Stem Growth and Development

The role of the stem in a crop plant is to raise the canopy of a crop and orientate leaves in an advantageous architecture for maximum light interception. Stems also provide a co-ordinated channel for movement of assimilates throughout the plant for the supply of water and mineral nutrients to the shoot, and for the redistribution of storage reserves. Despite these significant roles of the stem, it has been suggested that stem development may compete for assimilates. Consequently, breeding programs are presently being continued to minimize partitioning into stem tissues (Chandler, 1969; Donald and Hamblin, 1976).

Root Growth and Development

Root growth is complementary to shoot growth in the development of the vegetative plant structure. Roots are essential to the supply of

water and mineral nutrients, and they are found to account for 5 to 10 per cent of total primary production (Loomis and Gerakis, 1975).

Root to shoot ratios have been an expression indicating the importance of a balance between shoot and root development. Wareing and Patrick (1975) noted that roots supply certain other hormones plus certain other amino acids and carbohydrates to the roots. In general, the plant root must be established early in the life cycle of a crop. The presence of a large root system will determine the accessibility of water and mineral nutrients during plant growth and development.

Murata and Matsushima (1975) showed that root dry weight in rice declined at heading and similar reductions in root mass have been reported in many species. Russell (1977), in his book on plant root systems, recognized that roots and shoots increase in parallel during the vegetative phase, but that there is often a marked divergence in growth during transition to the reproductive phase.

Fruit Growth and Development

The entire physiology changes at flowering, and the transition from vegetative to reproductive development changes the pattern of assimilate distribution (Thornley, 1972). Fruit development becomes the major sink of assimilates in which the upper leaves supply the shoot apex, lower leaves supply the root, and intermediate leaves supply both positions (Wareing and Patrick, 1975). Upon fruiting, the entire partitioning changes, and the proximity of the sink becomes a more determining factor in its accumulation of assimilates (Thrower, 1962; Canny, 1972; Ismail and Sagar, 1981).

Yield and Harvest Index

The economic product of a crop may be root, stem, leaf, or typical-

ly, a reproductive organ. Recognition of the strong selection for the economic portion of the plant led to the development of the term "migration coefficient", a term which evolved into the concept of harvest index (Donald and Hamblin, 1976). Harvest index is the ratio of dry matter yield of the economic unit (harvest) to that of the total dry matter yield (biological yield) of the entire plant. Because the extraction of roots from the soil is a very tedious and inefficient process, root weights are generally not included in the measurements of harvest index. Exceptions to this general practice are those cases where the root is the economic product, as in the case of sugar beet or sweet potato, for example.

Harvest index reflects the efficiency of the distribution of assimilates into economic yields. It has been found that the bulk of the assimilate supplied to the developing root, fruit or grain sinks is from de novo synthesis; whereas, leaves, stems, and roots may store large quantities of reserves which they redistribute during fruit development, or during grain-filling of the seed (Yoshida, 1972; Donald and Hamblin, 1976).

Harvest index may be as low as 0 per cent in the case of complete crop failure, or as high as 100 per cent for the situation where the entire plant is the economic product, as in the case of most forages. Between these extremes, the situation is quite variable. According to Cooper (1975), the harvest index in cereals usually varies between 38 per cent and 55 per cent. Root and tuber crops have a larger range, from as low as 45 per cent to as high as 91 per cent.

Plant harvest index is a very important measurement in the assessment of productivity. Jennings and de Jesus (1968) observed a positive

correlation between harvest index and yield in rice. Similar results have been obtained for corn, wheat, barley, and other cereal crops (Evans and Wardlaw, 1976).

III. METHODS AND MATERIALS

The Effect of Plant Density on Yield

Plant Materials and Growing Conditions

'Autumn Pride' , a new bush cultivar of winter squash, was compared to 'Blue Hubbard', a high-yielding vine cultivar of Cucurbita maxima Duch. winter squash. 'Autumn Pride' has 'Hubbard' parentage and produces a large, pale-orange, Hubbard-type fruit. The 'Blue Hubbard' is similar in shape, but is blue-gray in color.

'Blue Hubbard' seeds were purchased from the Joseph Harris Co., Inc. of Rochester, New York. 'Autumn Pride' seeds were obtained from the breeding stock of Dr. Loy. 'Blue Hubbard' seeds averaged 0.33 gram each. 'Autumn Pride' seeds averaged 0.29 gram each. Germination tests on absorbent wadding gave a 95 per cent germination for 'Blue Hubbard' and a 65 per cent germination for 'Autumn Pride' during both test years.

Only healthy, vigorous seedlings were used as transplants. Furthermore, field stands were kept uniform by replacing dead or uprooted seedlings with new transplants.

1980 Experimental Design: A split block between 'Blue Hubbard' and 'Autumn Pride' formed the main treatments. The 'Autumn Pride' split consisted of sub-plots of four planting densities of 'Autumn Pride' plants. Four blocks formed the four replications.

Rows were 1.5 m apart, and planting density was varied by in-row spacing among plants. Bush plants were spaced 30 cm (1 ft.), 60 cm, 90 cm, and 120 cm apart. Vine plants were planted only at one spacing, 120 cm (4 ft.) apart. All main plots were 1600 m² and sub-plots were

400 m² in size. Two sets of guard rows were used around the 'Blue Hubbard' plots, and one row of guard plants surrounded each 'Autumn Pride' sub-plot. On the same day each week, data on crop development were taken. Four plants per treatment were randomly selected and used for the measurement of the lengths of the main stem, the number of leaves per plant, plant height, and the sizes of four fully expanded sun leaves. On two dates, lengths and diameters of developing fruits on four randomly selected plants in each treatment were also measured. Of these fruits, one fruit per treatment was randomly selected and sampled. The partitioning of dry matter into pericarp, seeds and placental material was determined.

Field Management: Seeding was on May 21, 1980, in Jiffy-7 peat pellets in the greenhouse. The field was broadcast fertilized with 800 pounds per acre of 15-15-15 and treated with diazinon insecticide for cutworm control prior to planting. Plants were transplanted into the field on June 5, 1980, and they were sprinkler irrigated 3 times during the growing season. Biweekly sprayings with mixtures of Sevin and Malathion were made to control insects. Beginning in July, Marlate and Benlate fungicides were applied at weekly intervals to control disease.

1981 Experimental Design: The 1981 plant density experiment was similar to that of 1980, except that 3 blocks were used instead of the 4 used in 1980. 'Blue Hubbard' and a phenotypically identical sister line to 'Autumn Pride' were compared.

Field Management: Fertilization and spraying schedules were the same as those used in 1980. Seeding was on May 22, 1981, in the greenhouse, and seedlings were transplanted into the field on June 3, 1981.

Growth and Partitioning of Dry Matter

Because 'Blue Hubbard' is not isogenic to 'Autumn Pride', some of the observed differences between bush and vine strains could be cultivar differences rather than differences due to plant phenotype. Thus, a vine phenocopy of the bush strain was produced by treatment of 'Autumn Pride' with gibberellic acid (GA_3). These GA_3 -treated plants formed a third treatment.

Greenhouse Experiment

Data from the 1980 field experiment indicated that there was significant difference in growth and partitioning between 'Autumn Pride' and 'Blue Hubbard' in the field. To compare vegetative growth and partitioning of dry matter between 'Autumn Pride' and 'Blue Hubbard', a greenhouse experiment was carried out.

Plant Materials and Methods: 'Autumn Pride' and 'Blue Hubbard' seeds were germinated in the dark in a growth chamber beginning on January 30, 1981. Upon emergence of the radicle on February 1, 1981, a 14-hour light and 10-hour dark cycle was used. Two days later, half of the germinated 'Autumn Pride' seedlings were wetted with 10^{-3} M gibberellic acid (GA_3). On February 4, 1981, the seedlings were transplanted into moist Cornell soil mix in 4-liter (8-inch) plastic pots. Greenhouse temperature was maintained at approximately $29^{\circ}C$ during the daytime and $23^{\circ}C$ during the nighttime.

Experimental Design: 'Autumn Pride' (bush), 'Blue Hubbard' (vine), and 'Autumn Pride' treated with 10^{-3} M GA_3 formed the three treatments. A randomized complete block design was used. A north-south oriented greenhouse bench was sub-divided into 5 blocks of 18 pots each. The blocking was to eliminate errors caused by variation in lighting of the

bench and to simplify sampling. Incandescent lighting was provided to extend the daylength to a constant 12 hours. Only main stem growth occurred during the course of the experiment.

On each sampling date, each plant was subdivided into leaf blade (lamina), leaf petiole, stem and root. The root (including the hypocotyl) was washed free of soil and blotted dry. Samples were weighed to obtain fresh weight data. They were then transferred into the oven where they were dried at 60° to 75°C for 48 hours. On the last sampling date, the lamina was removed, but all petioles were left attached to the main stem. The entire epicotyl minus the leaf blades was thus designated stem tissue.

Field Experiment

An experiment to compare the productivity and dry matter partitioning in 'Autumn Pride' and in 'Blue Hubbard' was carried out at the Woodman Horticultural Farm. An additional treatment was the bush plants sprayed with 10^{-4} M gibberellic acid to the time of transplanting and two weeks after transplanting.

Fertilization and pest control were the same as described for the 1980 trials.

The experiment consisted of the three treatments and five replications in a randomized complete block design. Biweekly sampling of plants was carried out to obtain data on the number of leaves, the length of main stems, plant height, and wet and dry weights of stems (including petioles), fruits, and leaves.

Samples were weighed in the field with a top-loading scale, and they were then transported to the greenhouse where they were oven-dried to a constant weight for 48 hours to one week at 65° to 75°C. Drying time was

variable because the bulkiness of plant materials varied after being packed into drying sacks. Evenness of drying of the sampled tissues was desirable for accurate comparison of dry weights.

Leaf Anatomy

Fully-expanded mature sun leaves from field-grown plants were selected for examination. Each leaf was severed near the base of its petiole with a single cut. Leaf petioles were then placed under water and recut to release trapped air and keep water movement in the leaf active and uninhibited. The leaves, with their petioles in water, were placed in a lighted growth chamber. From these turgid leaves, samples of leaf tissues were obtained within one hour after they were cut from the plant.

Leaf specimens were dropped into a formaldehyde-acetic acid and ethanol (FAA) solution for fixation. The solution was composed of 10 per cent formaldehyde (40%), 50 per ethanol (95%) and 10 per cent glacial acetic acid. Sections were kept in the solution for 24 or more hours for fixing.

Leaf samples were then dehydrated through a series of dilutions of ethanol, water and tertiary butyl alcohol solutions. Specimens were next removed and infiltrated with paraffin at 60°C for three days, and then stored in a refrigerator. Tissues were mounted on blocks from which they microtomed into ribbons with a single-edge razor blade.

Sets of 5 ribbon sections were then floated in Haupt's adhesive on a microscope slide. Each slide was warmed on an embedding plate and the sections were set into place. After the ribbons had adhered to the slides, the slides were then passed through a series of xylene-alcohol solutions and eventually stained with Safranin and Fast Green-FCF. The tissues were then mounted in Canada balsam adhesive and covered with

glass cover slips. After preliminary examination, the slides were stored for several days for drying.

Leaf tissues were examined for chloroplast arrangement, the presence of bundle sheaths, mesophyll cell arrangements, and general comparative anatomy.

The Determination of CO_2 Compensation Points

The method used in the determination of CO_2 compensation points for the bush and vine squash types is based on the laboratory technique presented by Ross (1974).

'Blue Hubbard' (vine) and 'Autumm Pride' (bush) winter squash leaves were compared. Corn leaves were used as a C_4 species check, and bean leaves were used as a C_3 species check. Three replications were set up; two replications were in 1000 ml flasks, and one replication was in 250 ml flasks. Each flask contained 10^{-4} M NaHCO_3 . Distilled water was added to each of 12 ten-ml vials, each having threaded necks. The terminal 10 cm from healthy young corn leaves were used, and the bases of the leaves were inserted into the vials. For squash and bean, a leaf was removed from the plant along with 5 cm of leaf petiole. Each petiole was placed into a 10 ml vial. A 60 cm thread was tied around the neck of each vial, and the vial was inserted into the Erlenmeyer flask, each vial hanging midway in the flask and holding a sample of the leaf type. A tight-fitting stopper held the vial on the string during the entire experiment.

The initial pH of the NaHCO_3 solution in the flask and the pH after the exposure of the leaf to light for three hours were measured. The concentrations of CO_2 was determined from standard pH versus CO_2 concentration curves (Ross, 1974) for the 30° growth chamber temperature.

A second experiment with a new set of leaves was run for 18 hours

to determine if CO_2 concentration could be reduced further. The pH was measured for each treatment. A third experiment used the same test leaves, but the leaves were kept in darkness for 6 hours, after which the pH of the NaHCO_3 solution in each flask was again measured.

Sink Proximity and the Rate of Mass Transfer

'Blue Hubbard' and 'Autumn Pride' were seeded in Cornell mix in ten-inch pots on June 1, 1981. On June 18, half of the germinated 'Autumn Pride' seedlings were treated with 10^{-3} M gibberellic acid. On June 22, the plants were set at 30 by 90 cm spacing in the greenhouse and used in a preliminary experiment.

Uniformly labelled ^{14}C -sucrose with a specific activity of 3.6 mCi per millimole (New England Nuclear Corporation) was used. Radiochemical purity was given as 98 per cent on May 23, 1980.

The preliminary experiment was carried out with 29-day old plants. The plants were treated with ^{14}C -sucrose containing 0.1 per cent dimethyl sulfoxide (DMSO). A 100 μl aliquot of 10^6 dpm of ^{14}C -sucrose was deposited on the basal end of the most fully expanded leaf. At one and a half hours after treatment, a first block of treatments was sampled. Twenty-four hours later, the second and third blocks were sampled. The activity in these samples were low, and the aliquot was increased to 2×10^6 dpm.

A second set of seeds was germinated in a laboratory growth chamber (30°C) on June 30, 1981, to secure evenly developed bush and vine plants. Seedlings were transplanted into six-inch pots on July 3, 1981.

A split plot design of five replications and completely randomized treatments was used. The treatment of either the fifth or the tenth leaf formed a split of each strain in a randomized complete block design.

Six weeks after transplanting, 2×10^6 dpm ^{14}C -sucrose solution, containing 0.1 per cent DMSO, was deposited either on the fifth or tenth fully-expanded leaf, leaf counts being made from the apex towards the base of the plant. Twenty-four hours after the leaves were fed, the plants were sectioned into source leaf (the leaf fed), the apex (including the first 3 nodes of the plant), the root, and the rest of the plant. The source leaf petiole was assayed separately from the leaf blade because the chlorophyll quench in the leaves was very significant, as will be discussed later. Upon sampling, dry weights of the various portions were determined. The radioactivity remaining in the source and sink tissues was then assayed.

To assay radioactivity in the various tissues, the dried tissues were ground, and 100 mg samples were digested in Oxifluor (New England Nuclear), a tissue solubilizer and scintillation solvent. Table 1 shows the liquid scintillation counting efficiency with the various tissues, as determined by the internal standardization method (Wang et al., 1975). After 24 hours of solubilization, the samples were counted in a Beckman-7000 liquid scintillation counter. From the differential counts established, the movement of translocates was determined.

In the winter of 1981, the treatments made in the summer were repeated. The same leaf positions and aliquots were used, except that there were four replications instead of five.

Table 1: Mean counting efficiencies, determined by the internal standardization method, of cocktails containing 100 mg of tissues from different squash organs, using the Beckman-7000 Liquid Scintillation Counter.

Organs	Mean Counting Efficiency (%)	
	'Autumn Pride'	'Blue Hubbard'
Leaf	4.6	2.4
Petiole	10.8	10.3
Apex	8.9	4.2
Root	7.1	6.3

IV. RESULTS

Crop Growth and Development in the Field

Elongation of the main stem, canopy architecture, leaf area index (LAI), flowering and fruit development, and yielding ability were compared between bush ('Autumn Pride') and vine ('Blue Hubbard') plants of winter squash. The patterns of growth and development of 'Autumn Pride' was found to be quite different from that of 'Blue Hubbard'.

Growth of the Main Stem

Stem elongation in 'Autumn Pride' (bush) plants was barely detectable during the first month of growth and remained well below the rate observed in 'Blue Hubbard' (vine) plants (Figure 1).

Among the different spacings of 'Autumn Pride' plants, stems were longer at higher plant densities during the latter part of the growing season (Figure 2). Main stems of plants spaced 120 cm apart averaged 55 ± 3.5 cm in 1980 and only 47 ± 2.9 cm in 1981. Main stems of plants spaced 30 cm apart averaged 70 ± 3.0 cm in 1980 and 73 ± 4.0 cm in 1981.

Canopy Development

'Blue Hubbard' plants produced leaves more rapidly than 'Autumn Pride' plants (Figure 3). As early as the second and third weeks after transplanting, 'Blue Hubbard' plants had significantly more leaves than bush plants, but differences were not accentuated until after the fifth week in the field.

Cumulative leaf production among bush plants was inversely correlated with plant density (Figure 4). Plants at the 30 cm in-row spacing had produced an average of 55 leaves at six weeks in the field. Produc-

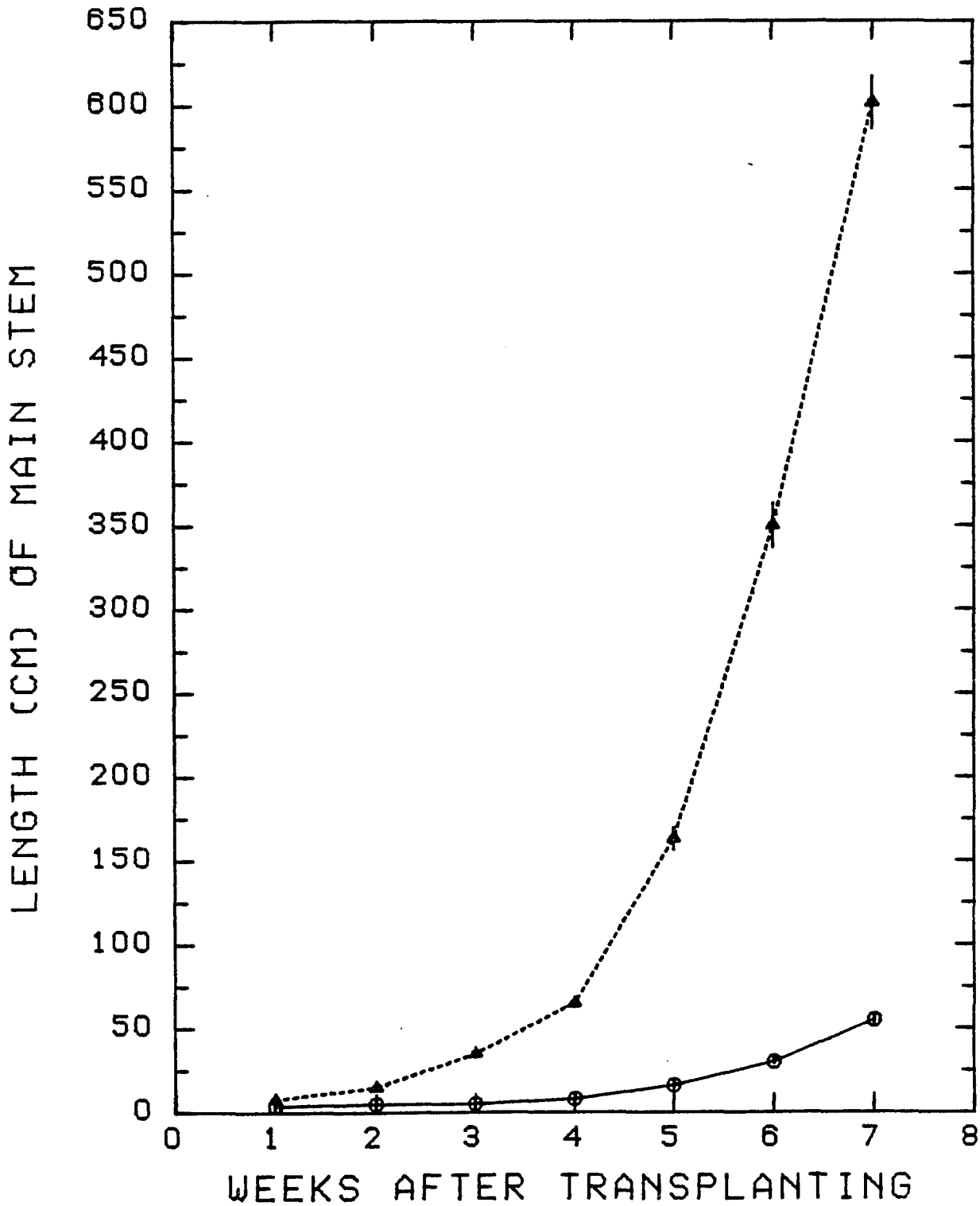


Figure 1: Comparative main stem lengths of 'Autumn Pride' (—) and 'Blue Hubbard' (-----), both at 5556 plants per hectare (1.2 x 1.5m) in the field in 1980. Values \pm SE bars represent means of four blocks, and four sample plants per treatment.

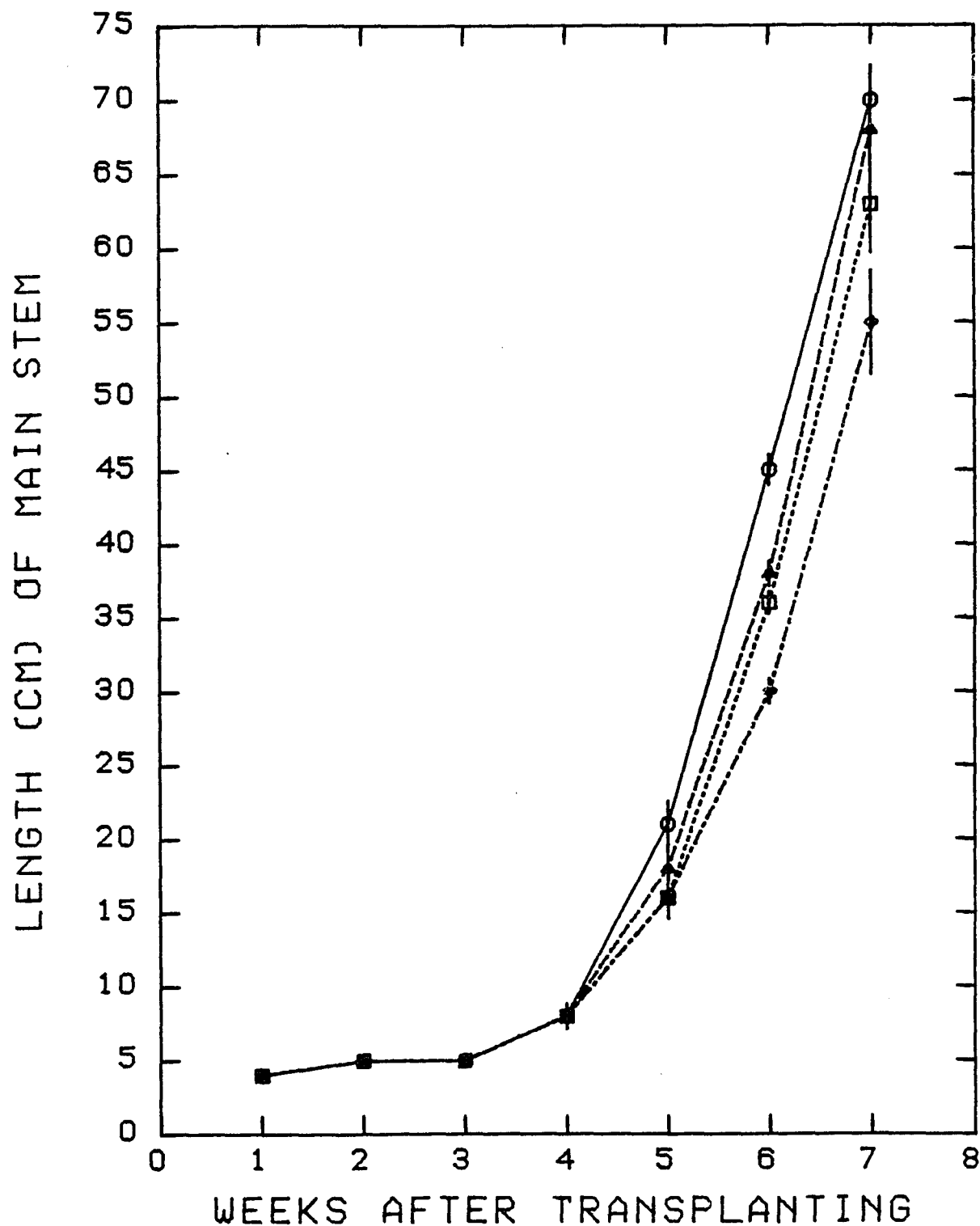


Figure 2: The growth of the main stem of 'Autumn Pride' at four plant densities in the field in 1980. 5556 pl/ha (---); 7407 pl/ha (.....); 11,111 pl/ha (-.-.-); and 22,222 pl/ha (—).

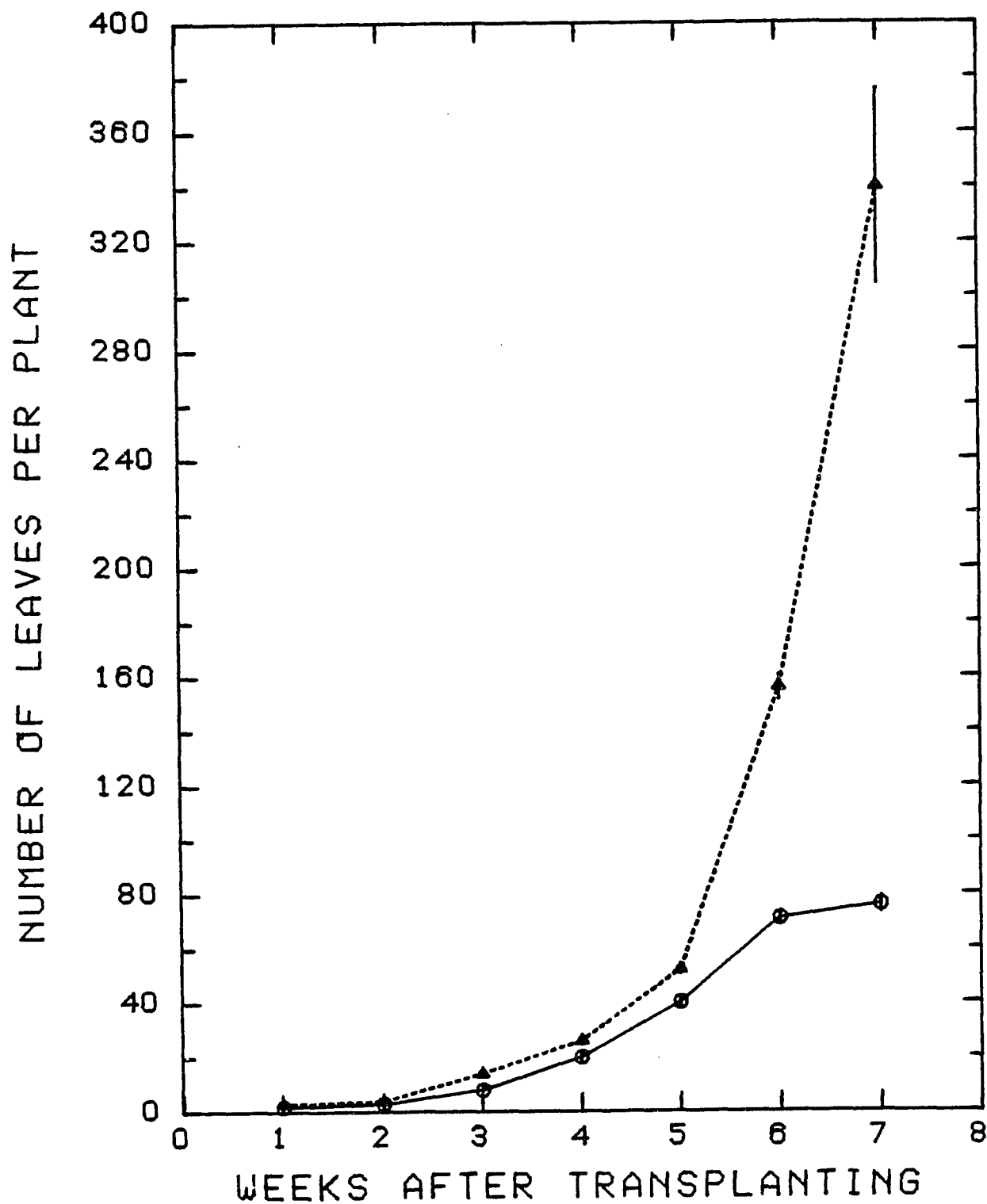


Figure 3: Comparative leaf development between 'Autumn Pride' (—) and 'Blue Hubbard' (-----) at 5556 pl/ha (1.2 x 1.5m) in the field in 1980. Values \pm SE represent means of four blocks, four sample plants per plot.

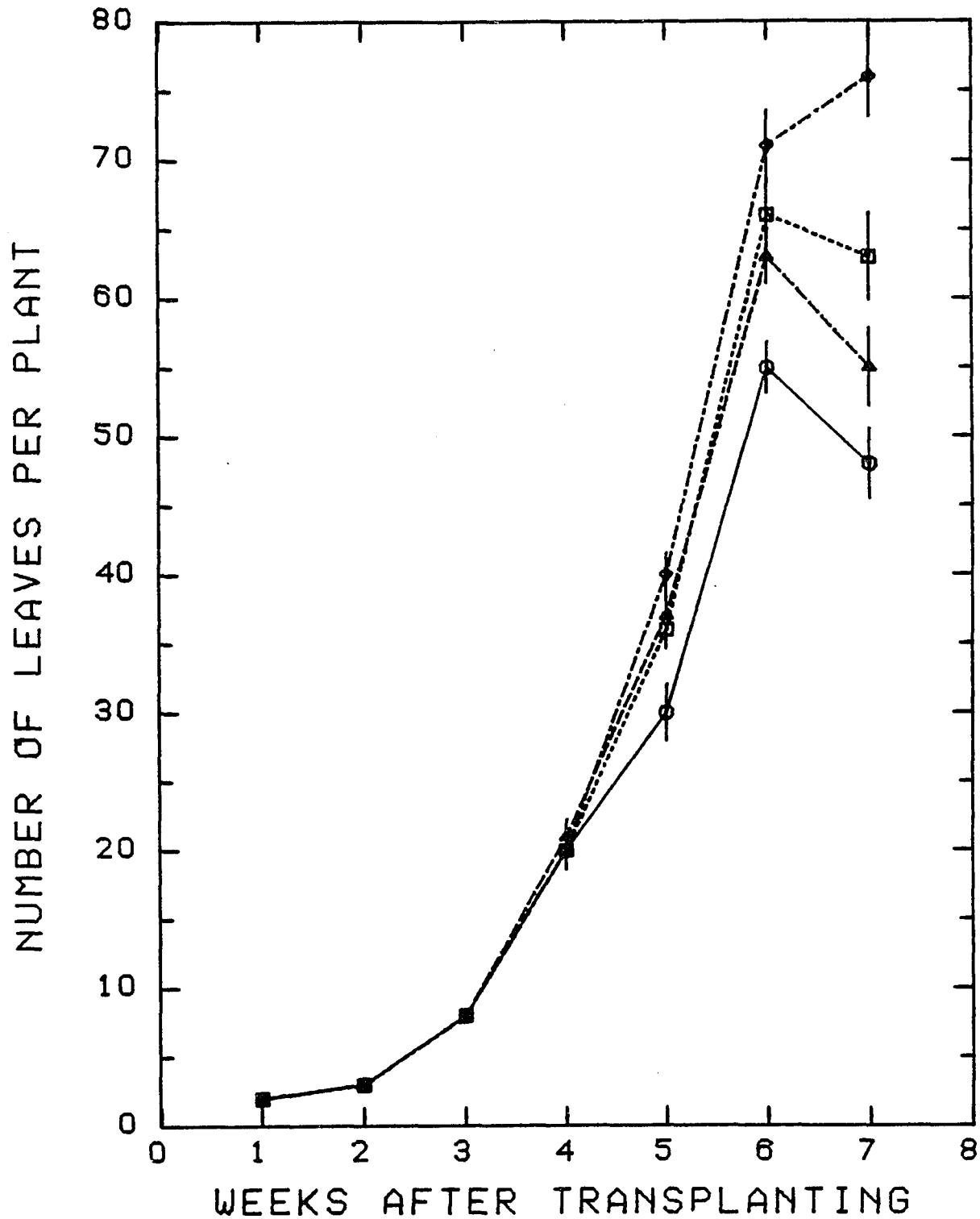


Figure 4: The production of leaves by 'Autumn Pride' at four plant densities in the field, in 1980. 5556 pl ha⁻¹ (—○—); 7407 pl ha⁻¹ (—□—); 11,111 pl ha⁻¹ (—△—); and 22,222 pl ha⁻¹ (—◇—). Values \pm SE represent means of four blocks, four sample plants per plot.

tion at other in-row spacings were 63 leaves at 60 cm, 66 leaves at 90 cm, and 71 leaves at 120 cm. This compares with an average production of 156 leaves per plant in 'Blue Hubbard'.

Figure 4 also shows that at higher plant densities, 'Autumn Pride' plants exhibited a net loss of leaves after the sixth week in the field. Only at the 120 cm spacing did the number of leaves per plant increase into the seventh week after planting.

Leaf Area Index (LAI): Leaf area indices were determined for 'Autumn Pride' at its four plant densities, and for 'Blue Hubbard' at its optimal planting density. Although it was shown that 'Blue Hubbard' (vine) plants had a larger number of leaves, LAI's for 'Autumn Pride' (bush) plants were significantly higher than LAI's for 'Blue Hubbard' (vine) plants over the first six weeks of growth (Figure 5). Later during the season, the LAI for vine plants exceeded 9.0, whereas the peak LAI for the bush plants was about 6.0.

The highest LAI's among 'Autumn Pride' plants were found at the highest density plantings. Peak LAI's for the 30 cm, 60 cm, 90 cm, and 120 cm in-row spacings were 6.02, 4.39, 3.49, and 3.04, respectively. Peak LAI's were reached at six weeks for the higher plant densities, but at seven weeks for the low plant density. The decline in LAI's at 6 and 8 weeks was due to senescence of older leaves and limited production of new leaves in bush plants at this stage of development.

Plant Height: The canopy height, the distance from the ground to the highest point on the plant, was determined by the length of the petiole, the length of the lamina of the leaf and the distance of the node above the ground at which the petiole was attached to the stem. Canopy heights progressively increased until 8 to 9 weeks from transplanting

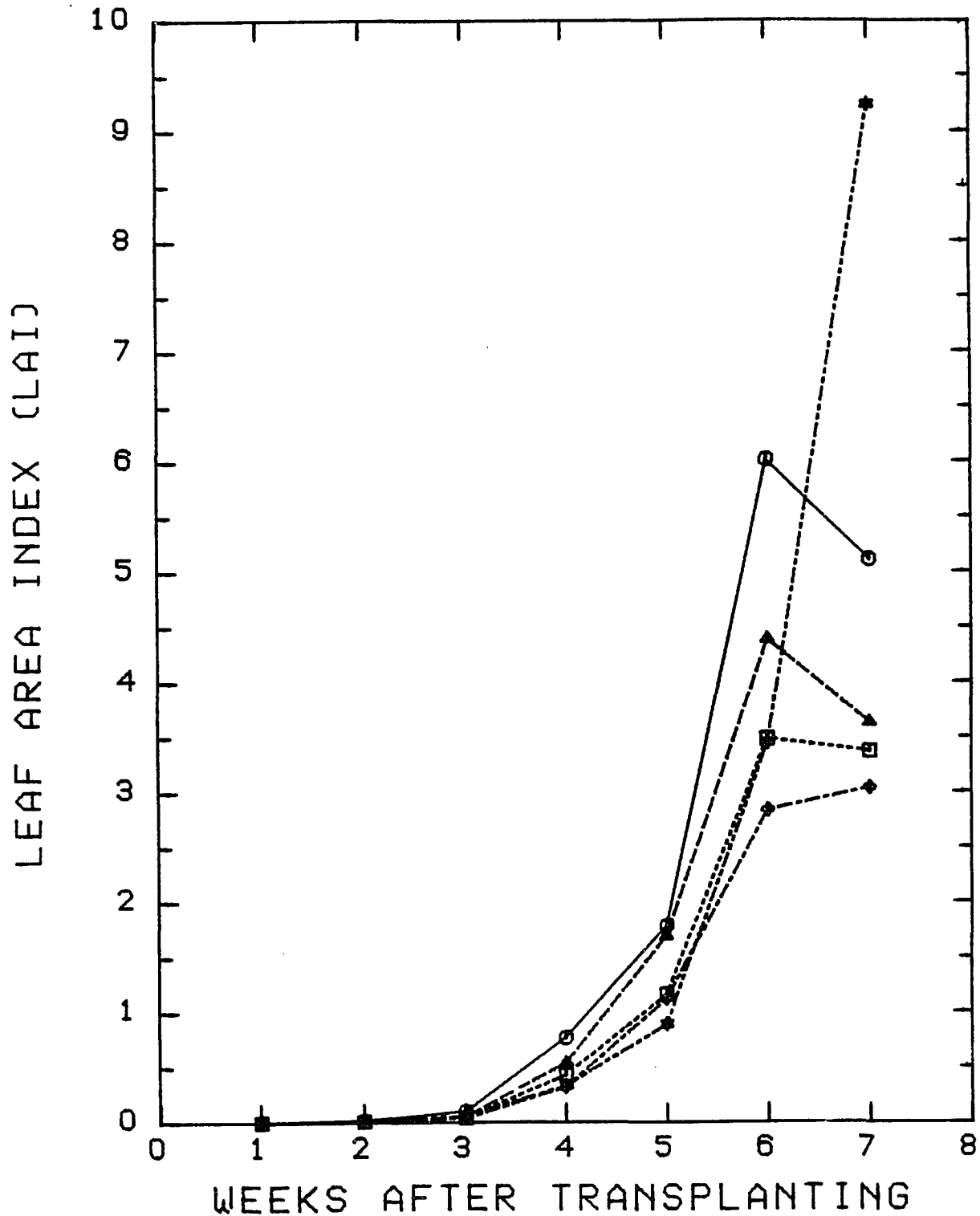


Figure 5: The effect of plant density on leaf area index (LAI) of 'Autumn Pride' at four plant densities in comparison to LAI of 'Blue Hubbard' (---★---) at its near optimal plant density (5556 pl/ha) in 1980. For 'Autumn Pride', 5556 pl/ha (---○---); 7407 pl/ha (---□---); 11,111 pl/ha (-.-△-.); and 22,222 pl/ha (—●—). Values represent determinations from four blocks, with four plant samples per treatment per block.

(Figure 6). The canopy of vine plants was lower than that of bush plants at all plant densities of bush plants.

Among bush plants, canopy height increased with increase in planting density (Figure 6). At 9 weeks after transplanting into the field, plant height at the 0.3 x 1.5 m spacing averaged 140 cm and at 1.2 x 1.5 m spacing averaged 132 cm.

The results were similar in 1981. The highest density plants were 138 cm tall, and those at the lowest density averaged 122 cm tall at 7 weeks after transplanting into the field.

Fruit Development and Yield

Economic Yield

Total fresh weights of fruits per hectare are given in Table 2. The highest fresh weight yields in 1980 and 1981 were obtained by 'Autumn Pride' at 0.3 x 1.5 m spacing. Plants at the 0.6 x 1.5 m and 0.9 x 1.5 m spacings also gave significantly higher yields than 'Blue Hubbard'. At the 1.2 x 1.5 m spacing, yields of 'Blue Hubbard' and 'Autumn Pride' were not significantly different.

At the 120 cm in-row spacing, mean fruit weights of 'Autumn Pride' and 'Blue Hubbard' were not significantly different. Among the bush plants, fruit mass declined with increasing plant density (Table 2).

'Autumn Pride' fruits were uniform in size and shape, but fruit lengths decreased from an average of 42 cm long at 1.2 x 1.5 m spacing to 29 cm long at 0.3 x 1.5 m spacing. Fruit diameter also decreased from 28 cm to 17 cm with increase in plant density. Fruits from 'Blue Hubbard' plants were variable in size and shape. There were many 'Blue Hubbard' fruits scarred by their own vines.

'Autumn Pride' fruits from the 30 cm spacing were not the most

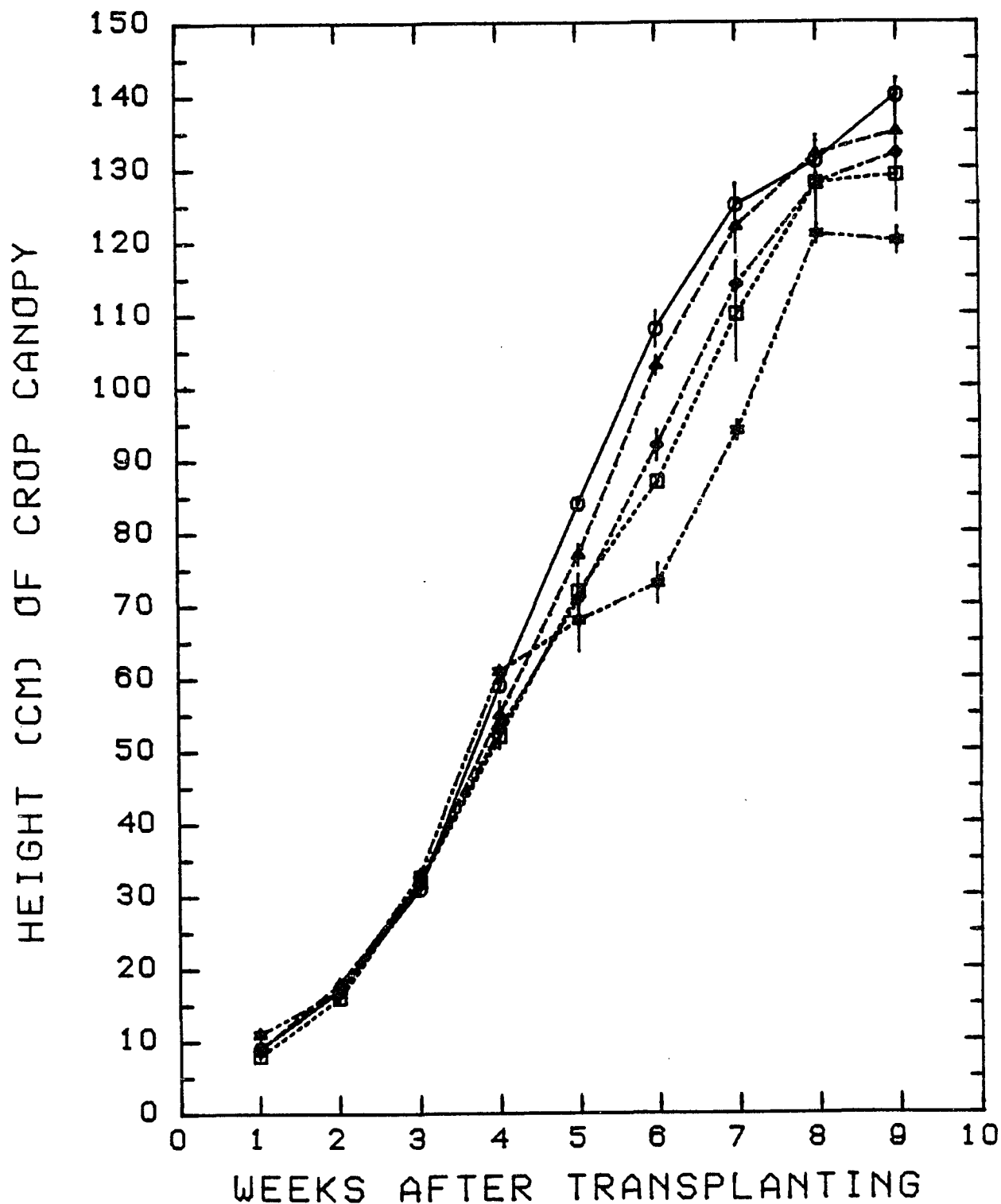


Figure 6: The effect of plant density on the canopy height of 'Autumn Pride' at four plant densities in comparison to the canopy height of 'Blue Hubbard' (-----) at its near optimum plant density in 1980. Values represent determinations from four blocks, with four plant samples per treatment per block. Designations for 'Autumn Pride' are 5556 pl/ha (.....); 7407 pl/ha (-----); 11,111 pl/ha (----); and 22,222 pl/ha (——).

Table 2: The effect of plant density on fresh weight fruit yield of 'Autumn Pride' at four plant densities, as compared to 'Blue Hubbard' at its near-optimum plant density. Between-row spacing was kept constant at 1.5 m for all treatments.

In-row plant Spacing (cm)	Plant Density (pl/ha)	1980				1981			
		(kg/ha)	(kg/pl	±	SE)	(kg/ha)	(kg/pl	±	SE)
'Autumn Pride'									
30	22,222	77,700 a ^z	3.7	±	0.2	74,500 a ^z	3.5	±	0.1
60	11,111	70,300 a,b	6.6	±	0.3	61,500 b	5.5	±	0.1
90	7,407	64,600 b,c	9.0	±	0.4	55,300 c	7.7	±	0.1
120	5,556	61,300 b,c	10.6	±	0.4	52,200 c,d	9.2	±	0.2
'Blue Hubbard'									
120	5,556	57,300 c	10.4	±	0.4	50,700 d	8.2	±	0.2

^zMean separation within columns by Duncan's Multiple Range Test, 5 % level.

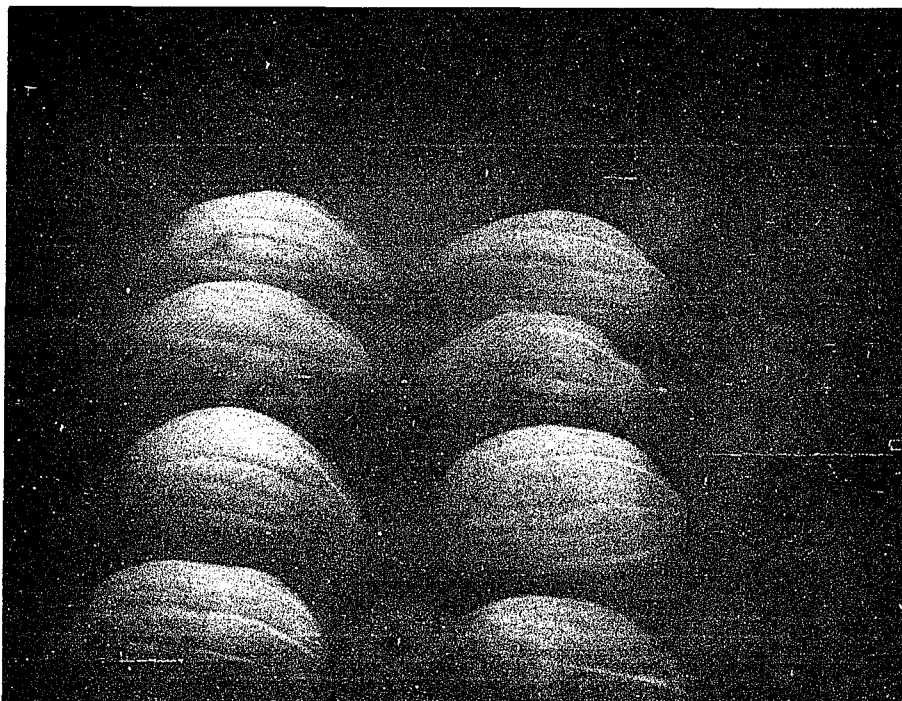
marketable, although yields at this spacing were the highest. Many were misshapen and poorly colored. Dark-green chlorophyll-colored patches were observed on many of these fruits. Some of the oddly colored fruits are shown in Figure 7. Fruits from the 60 cm, 90 cm, and 120 cm spacing were all uniform and marketable.

The per cent dry weight of 'Blue Hubbard' fruits was significantly higher than that of 'Autumn Pride' fruits at all plant densities. Per cent dry weight of 'Autumn Pride' fruits decreased with increase in plant density, and this affected the total biomass produced per hectare (Table 3). The highest biomass produced was at the $22,222 \text{ pl ha}^{-1}$ density for 'Autumn Pride'. 'Blue Hubbard' often produced more than one fruit per plant. The fruit which was set later was much smaller than the first fruit set, and its per cent dry weight was also much lower. Biomass production in 'Blue Hubbard' was also high due to the high per cent dry weight of its fruits.

The partitioning of assimilate within the fruit is an important facet of yield. The cavity of the squash fruit contains placental material and seeds. Fruits of the vine plants had 20.0 ± 5.5 per cent of their dry weight partitioned into placental material (seeds plus placental tissue), whereas fruits of 'Autumn Pride' plants had only 7.2 ± 2.9 per cent of their dry weight partitioned into placental material. In addition, the rind of 'Blue Hubbard' fruits formed a larger proportion of the fruit refuse than the rind of 'Autumn Pride' fruits.

Biomass Accumulation

In 1981, plant vegetative biomass was measured among plants in the spacing trial (Table 4). With increase in plant density among bush plants, fresh weight of individual plants decreased. The fresh weight



A. Examples of different sizes of 'Autumn Pride' fruits from the various plant densities.



B. Examples of poorly-colored fruits (ends) and normal-colored fruits (center) of 'Autumn Pride', seen at 22,222 pl/ha in the field.

Figure 7: Examples (A) of different sizes of 'Autumn Pride' fruits from various plant densities, and examples (B) of poorly-colored fruits (ends) and normal-colored fruits (center) of 'Autumn Pride', seen at 22,222 pl/ha in the field in 1980 and 1981.

Table 3: Dry weight yields and per cent dry matter in fruits of 'Autumn Pride' at different plant densities and 'Blue Hubbard' at its near-optimum plant density in 1981. Between-row spacing was constant at 1.5 m.

In-row Spacing (cm)	Plant Density (pl/ha)	Per Cent Dry Weight (% \pm SE)	Yield (kg/ha)
'Autumn Pride'			
30	22,222	7.1 \pm 0.3	5,302
60	11,111	7.4 \pm 0.8	4,551
90	7,403	7.8 \pm 0.4	4,313
120	5,556	8.8 \pm 0.2	4,594
'Blue Hubbard'			
120	5,556	9.6 \pm 0.2	4,861

Table 4: Total plant fresh weight yields for 'Blue Hubbard' at a near optimum plant density and 'Autumn Pride' at four plant densities.

In-row Spacing (cm)	Plant Density (pl/ha)	Vegetative Fresh Weight (kg \pm SE)	Total Fresh Weight (kg/pl)	Total Fresh Weight (kg/ha)	Harvest Ratio (%)
'Autumn Pride'					
30	22,222	0.64 \pm 0.18	4.14	89,010 ^z	85
60	11,111	1.27 \pm 0.43	6.73	72,684	82
90	7,407	2.23 \pm 0.57	9.93	71,498	78
120	5,556	3.50 \pm 0.42	12.60	68,040	73
'Blue Hubbard'					
120	5,556	5.27 \pm 0.61	13.97	75,430	62

^zDetermined from total fruit and vegetative fresh weight yields.

of 'Blue Hubbard' plants was significantly larger than that of bush plants at the same plant density. An estimate of total fresh weight produced per hectare is also presented.

Finally, it should be pointed out that fruits of 'Autumn Pride' matured about 5 days earlier than those of 'Blue Hubbard'. Thus biomass accumulation in bush plants occurred over a shorter period than with vine plants.

Vegetative Growth and Partitioning of Dry Weight

Greenhouse Experiment

Plant Morphology: Figure 8 shows the growth of main stems of bush ('Autumn Pride'), vine ('Blue Hubbard'), and GA_3 -treated 'Autumn Pride' plants. The main stems of vine plants were about ten times longer than the main stems of bush plants. Although GA_3 -treated plants were not as tall as vine plants, the effect of GA_3 on the elongation of the main stem of bush plants was dramatic. The effect of a single application of GA_3 during seed germination persisted throughout the seven weeks of growth.

Leaves of bush plants were fully-expanded, but fewer in number than those of vine plants. Bush plants also had shorter internodes than vine plants, and they did not need to be supported on stakes as did vine plants during their development in the greenhouse. Longer petioles and more angled leaf laminae were also characteristic of bush plants.

GA_3 -treated 'Autumn Pride' plants had both more leaves and longer internodes than untreated bush plants. Although GA_3 -treated 'Autumn Pride' plants exhibited the general morphology of 'Blue Hubbard' vine plants, they were not exact phenocopies, and they tended to display smaller leaves and spindly stems.

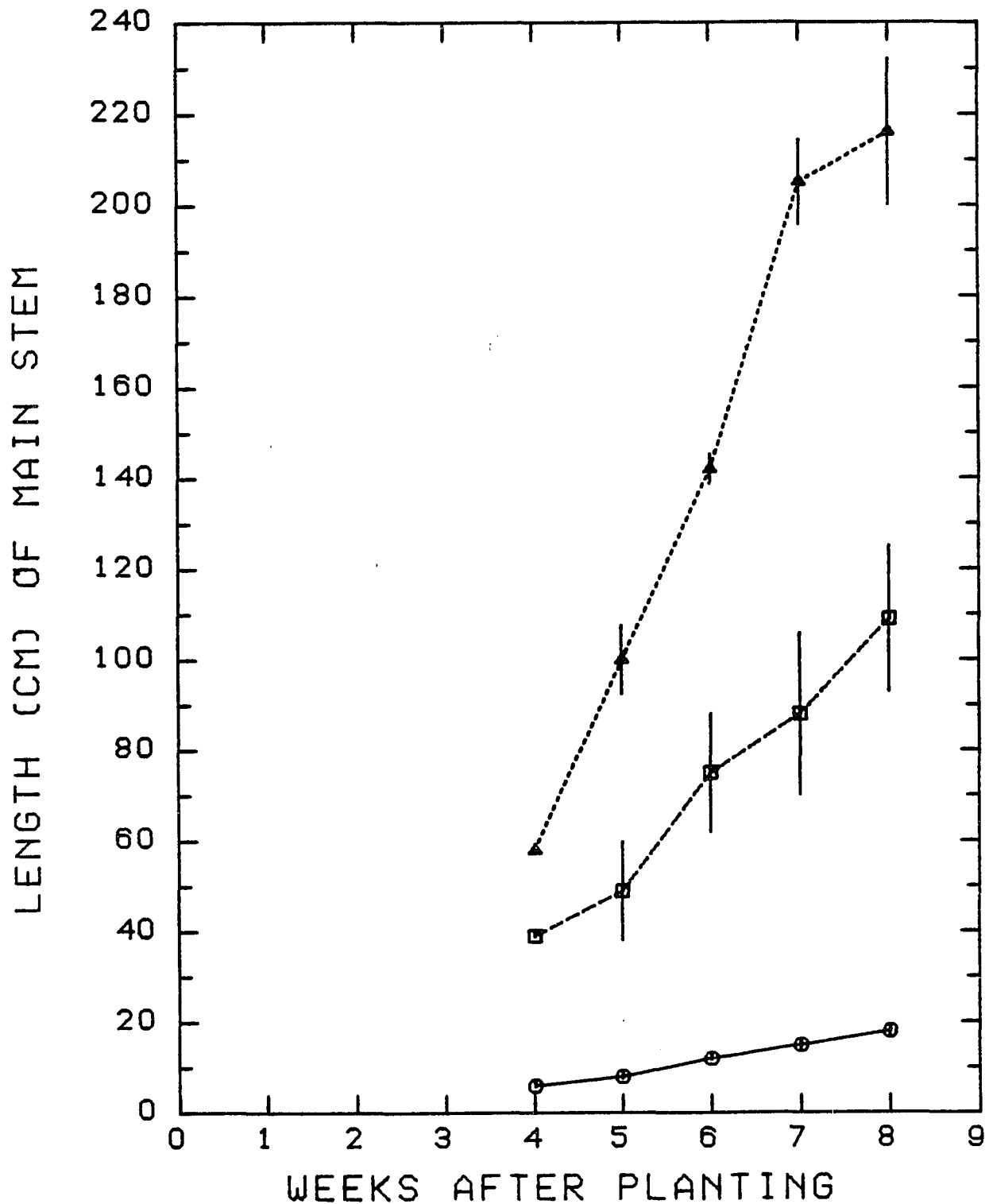


Figure 8: Comparative main stem lengths of 'Autumn Pride' (—), 'Blue Hubbard' (-----), and GA₃-treated 'Autumn Pride' (----) during their growth in the greenhouse. Values \pm SE represent means of five blocks, three samples per block.

Partitioning of Dry Matter: Total dry matter accumulated in plants grown in the greenhouse was quite similar for both 'Autumn Pride' and 'Blue Hubbard' (Figure 9), but distribution of dry weight among the various tissues was found to be different. 'Autumn Pride' plants deposited more of its dry weight into its leaves and roots than 'Blue Hubbard' and less into its stem tissues (Figure 10). GA_3 -treated plants of 'Autumn Pride' were intermediate to bush and vine plants in terms of dry matter distribution.

The greatest mass of roots among the three treatments was found among bush plants (Figure 11). Root mass in the GA_3 -treated 'Autumn Pride' plants and 'Blue Hubbard' were similar.

Stem dry weights were higher in 'Blue Hubbard' plants than in either 'Autumn Pride' or GA_3 -treated plants (Figure 12). Dry weights of total stem tissues (stem + petiole) were quite similar for 'Autumn Pride' and 'Blue Hubbard' (Figure 13). Stems of GA_3 -treated plants were abnormally spindly during early development as reflected by lower dry matter accumulation. The similarity in total stem tissue dry weight was due to the fact that petioles of bush plants had a considerably higher mass than those of the vine and GA_3 -treated bush plants and were classified as stem tissue.

Over the period of growth in the greenhouse, total mass of leaves in 'Autumn Pride' and 'Blue Hubbard' plants were not significantly different, except at the eighth week when the leaf mass of 'Autumn Pride' was significantly larger (Figure 14). Data on specific leaf weight (SLW) were taken at 8 weeks for leaves at the fifth node from the cotyledon. Vine plants had significantly lower specific leaf weight than either bush plants or GA_3 -treated bush plants. Leaf areas were estimated from SLW

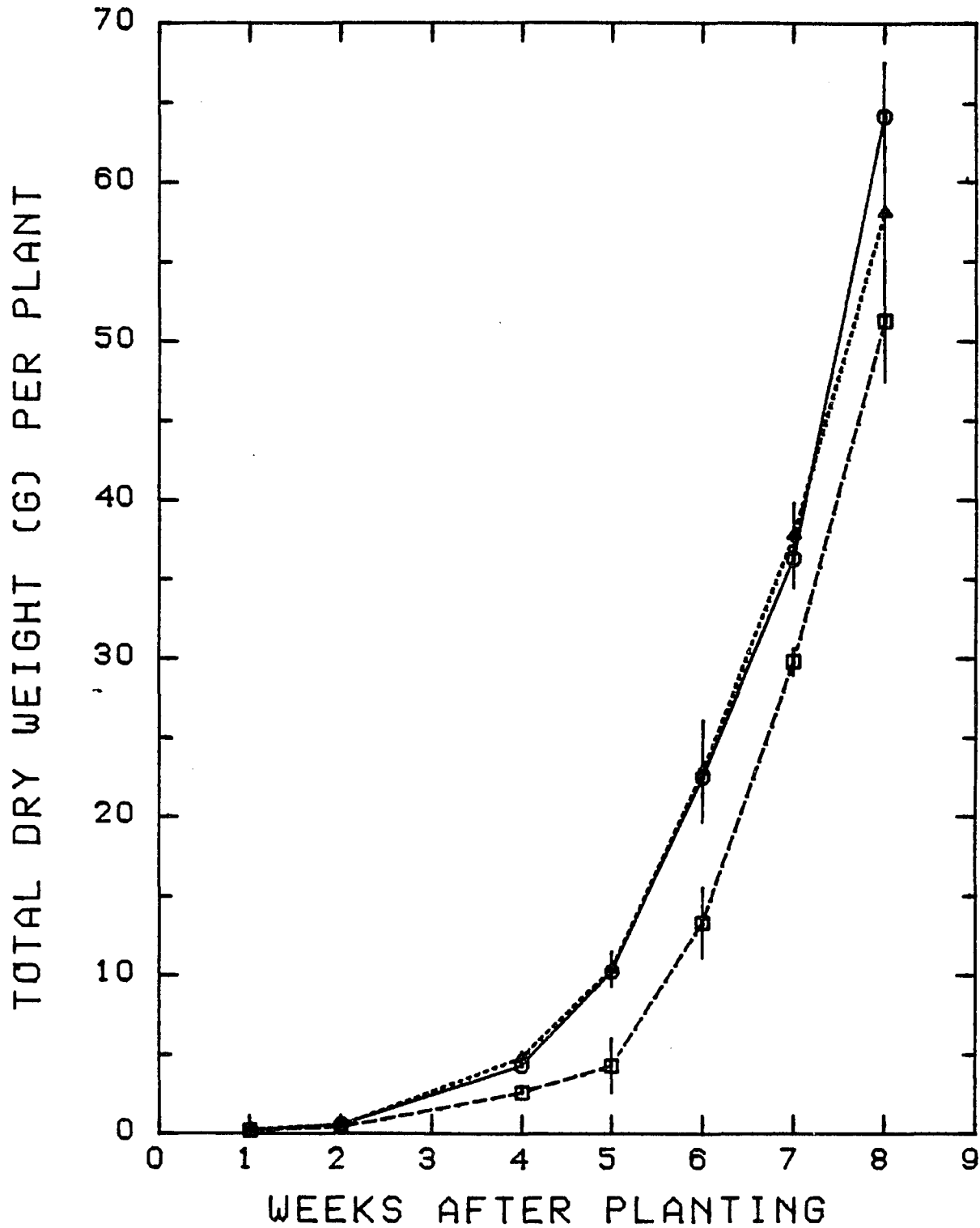


Figure 9: A comparison of total dry matter accumulation in 'Autumn Pride' (—), 'Blue Hubbard' (-----), and GA₃-treated 'Autumn Pride' (----) plants grown in the greenhouse.³ Values represent means \pm SE of five blocks, three samples per block.

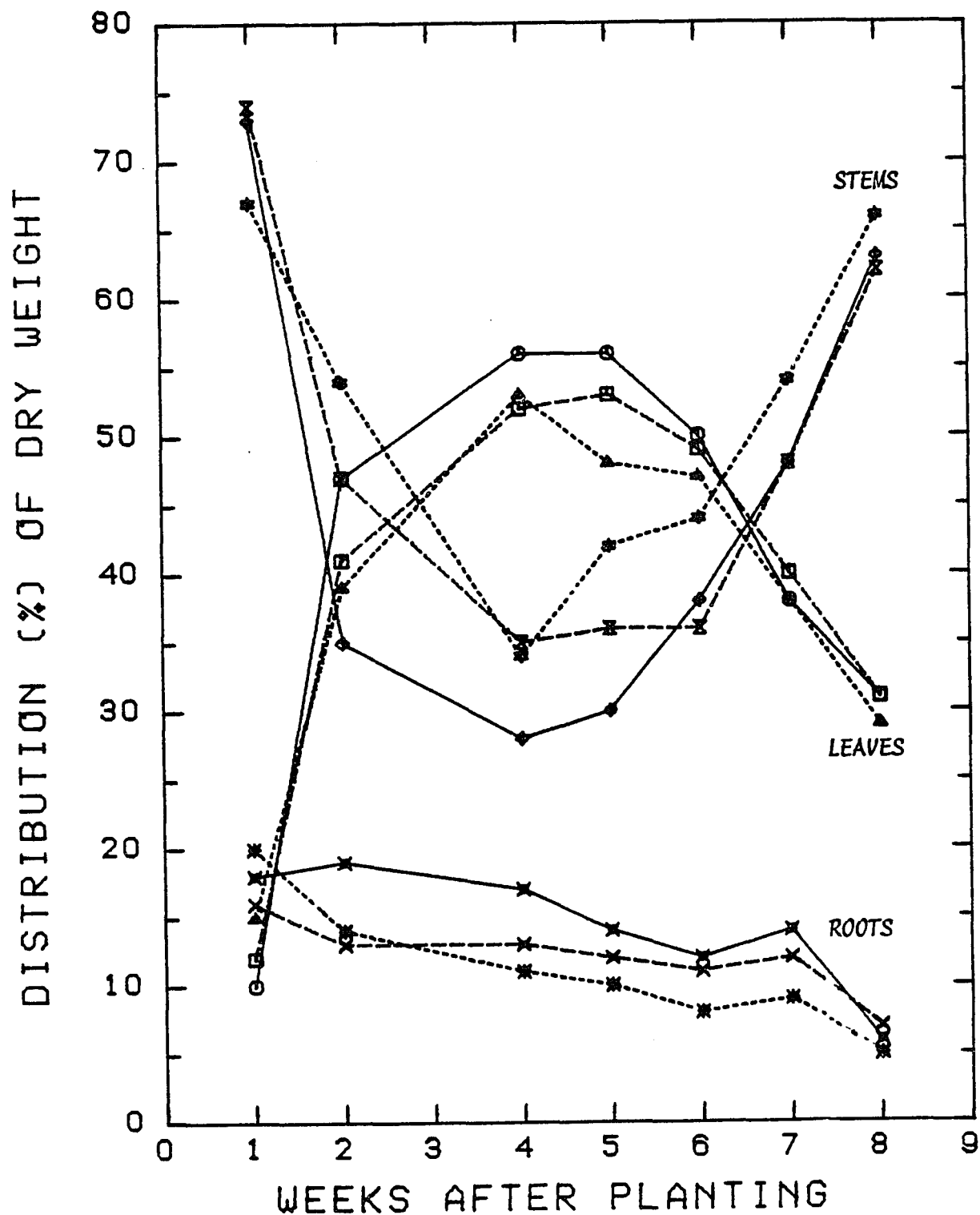


Figure 10: The partitioning of dry weight among roots, stems and leaves in 'Autumn Pride' (—), 'Blue Hubbard' (.....), and GA₃-treated 'Autumn Pride' (---) plants grown in the greenhouse. Values represent means - of five blocks, three replicates per block.

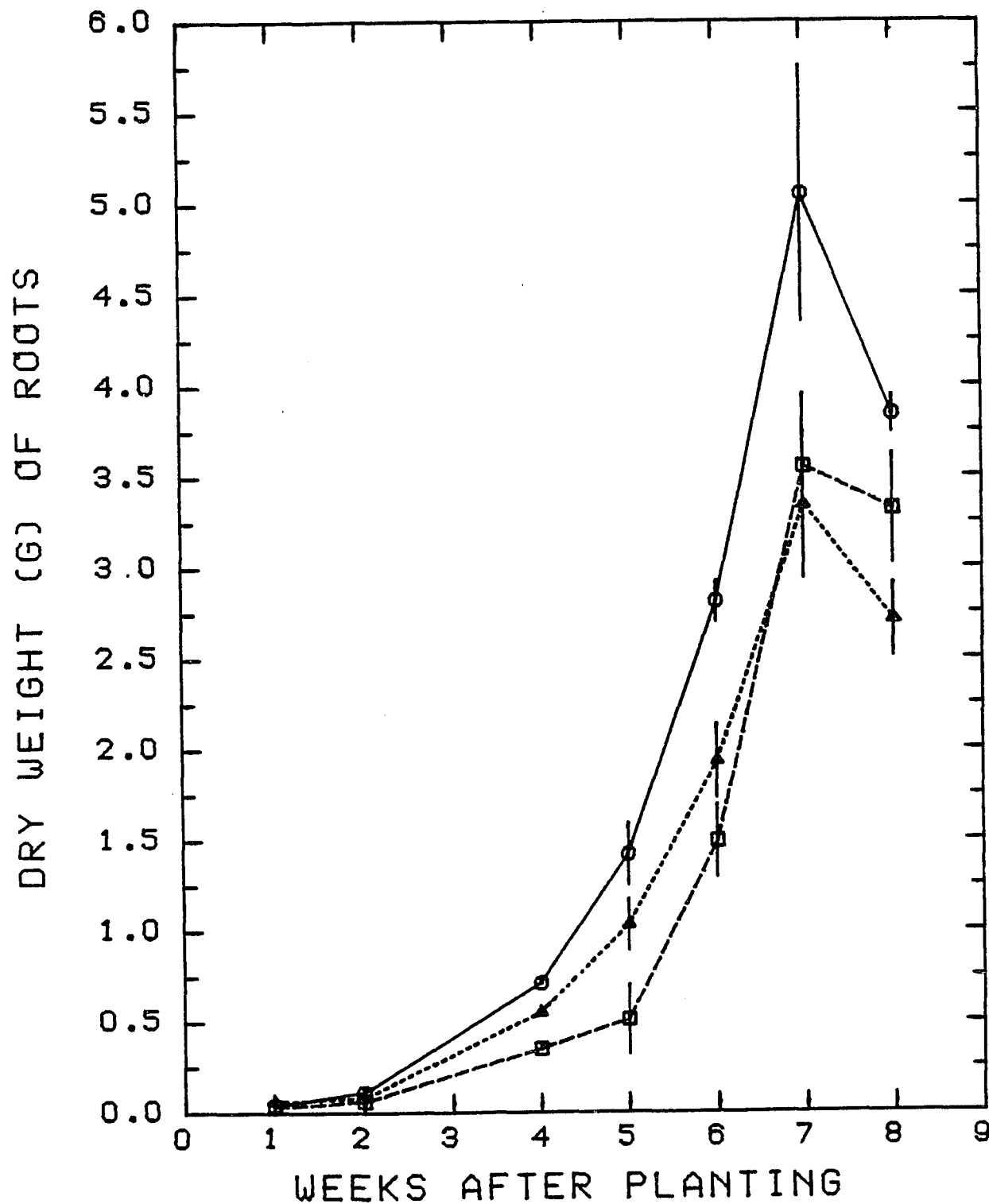


Figure 11: The accumulation of and loss of dry weight in roots of 'Autumn Pride' (—), 'Blue Hubbard' (-----), and GA₃-treated 'Autumn Pride' (---) plants grown in the greenhouse. Each value represents the mean \pm SE of five blocks, three replicates per block.

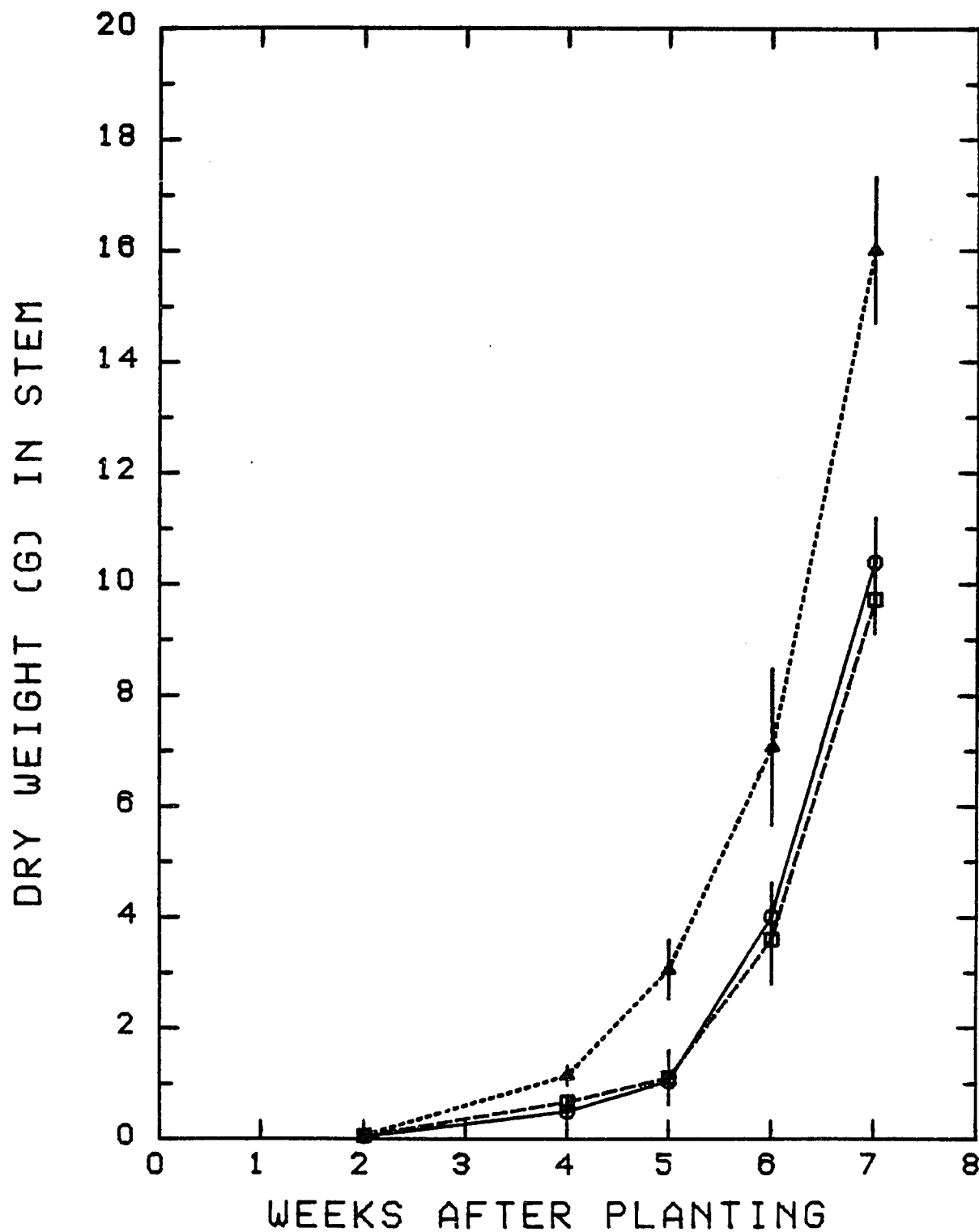


Figure 12: The dry weight of stems of 'Autumn Pride' (—), 'Blue Hubbard' (.....), and GA₃-treated 'Autumn Pride' (---) plants during their growth in the greenhouse. Values represent mean \pm SE of five blocks, 3 replicates per block.

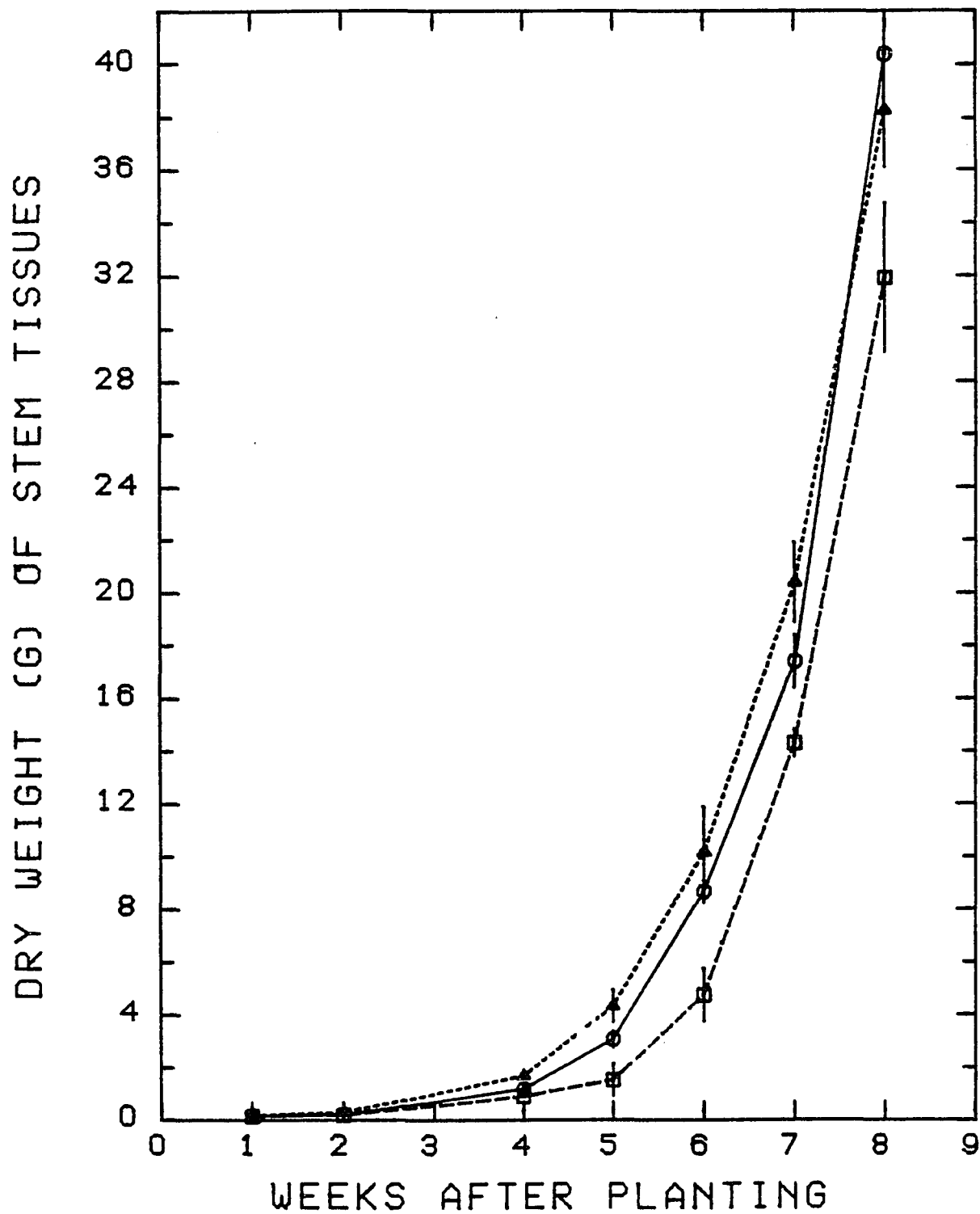


Figure 13: The accumulation of dry weight in stem tissues (stem + petiole) of 'Autumn Pride' (—), 'Blue Hubbard' (·····), and GA₃-treated 'Autumn Pride' (---) plants grown in the greenhouse. Values represent means \pm SE of five blocks, three replicates per block.

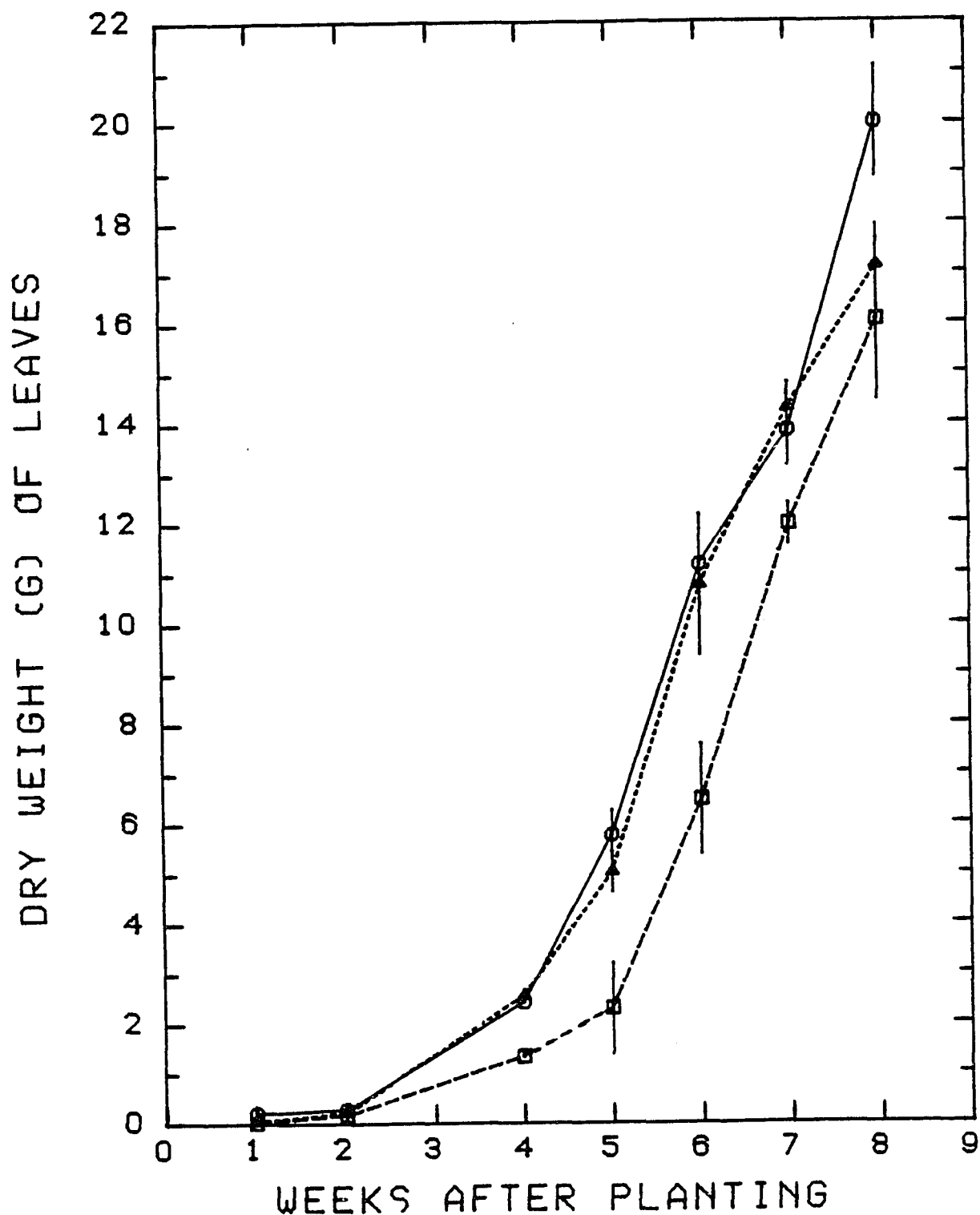


Figure 14: A comparison of dry weights accumulated in leaves of 'Autumn Pride' (—), 'Blue Hubbard' (.....), and GA₃-treated 'Autumn Pride' (---) plants grown in the greenhouse. Values represent mean \pm SE of five blocks, three replicates per block.

and total leaf weights and the total leaf area of 'Blue Hubbard' plants was significantly larger than that of 'Autumn Pride'. 'Autumn Pride' plants had a higher total plant dry matter and a lower leaf area ratio (LAR), indicating a higher efficiency of assimilation for this winter squash cultivar (Table 5).

Partitioning of Dry Weight at Low Density Planting in the Field

This study was conducted to extend greenhouse observations to field conditions under which partitioning of dry matter could be determined for both vegetative and reproductive phases of growth. Low density planting provided for the evaluation of dry matter distribution without the interactions of plant competition found in typical field plantings. Low density planting thus provides an estimate of maximum biomass production per plant and permits a complete assessment of plant morphology, distribution of dry weight, and potential size of plants, using techniques of growth analysis.

Total biomass accumulation in 'Autumn Pride' and 'Blue Hubbard' were the same throughout the first eight weeks of development (Figure 15). This corroborated the results obtained for the vegetative growth phase in the greenhouse. The GA₃-treated 'Autumn Pride' plants accumulated less dry weight over time than either vine or bush plants.

There were marked differences between bush and vine plants in the distribution of dry weight among various vegetative organs. Growth of leaves and stems peaked at the eighth week of development of 'Autumn Pride' while growth of stems and leaves in 'Blue Hubbard' continued through 12 weeks. Differentiation of multiple branch stems with adventitious roots in 'Blue Hubbard' led to greater production and more biomass in stems and leaves. The proportion of total biomass in stems and

Table 5: A comparison, at eight weeks after planting, of specific leaf weight (SLW), leaf dry weight, total plant dry weight, and leaf area ratio (LAR) among 'Autumn Pride', 'Blue Hubbard' and GA₃-treated 'Autumn Pride' plants grown in the greenhouse.

Factor	'Autumn Pride' (Bush)	'Blue Hubbard' (Vine)	GA ₃ -treated 'Autumn Pride' (Vine Phenocopy)
Specific Leaf Weight (mg/cm ²)	0.51 ± 0.02 ^z	0.38 ± 0.03 ^z	0.45 ± 0.02 ^z
Total Leaf Dry Weight (g)	20.00 ± 1.1	17.30 ± 0.8	16.10 ± 1.7
Total Leaf Area (dm ²)	39 ± 1	46 ± 4	36 ± 4
Total Plant Dry Weight (g)	64.2 ± 2.5	58.1 ± 3.0	51.3 ± 3.8
Leaf Area Ratio (cm ² /g)	6.1 ± 0.1	8.0 ± 0.7	7.9 ± 0.8

^zEach value represents means of 5 replicates and their associated standard errors (± SE)

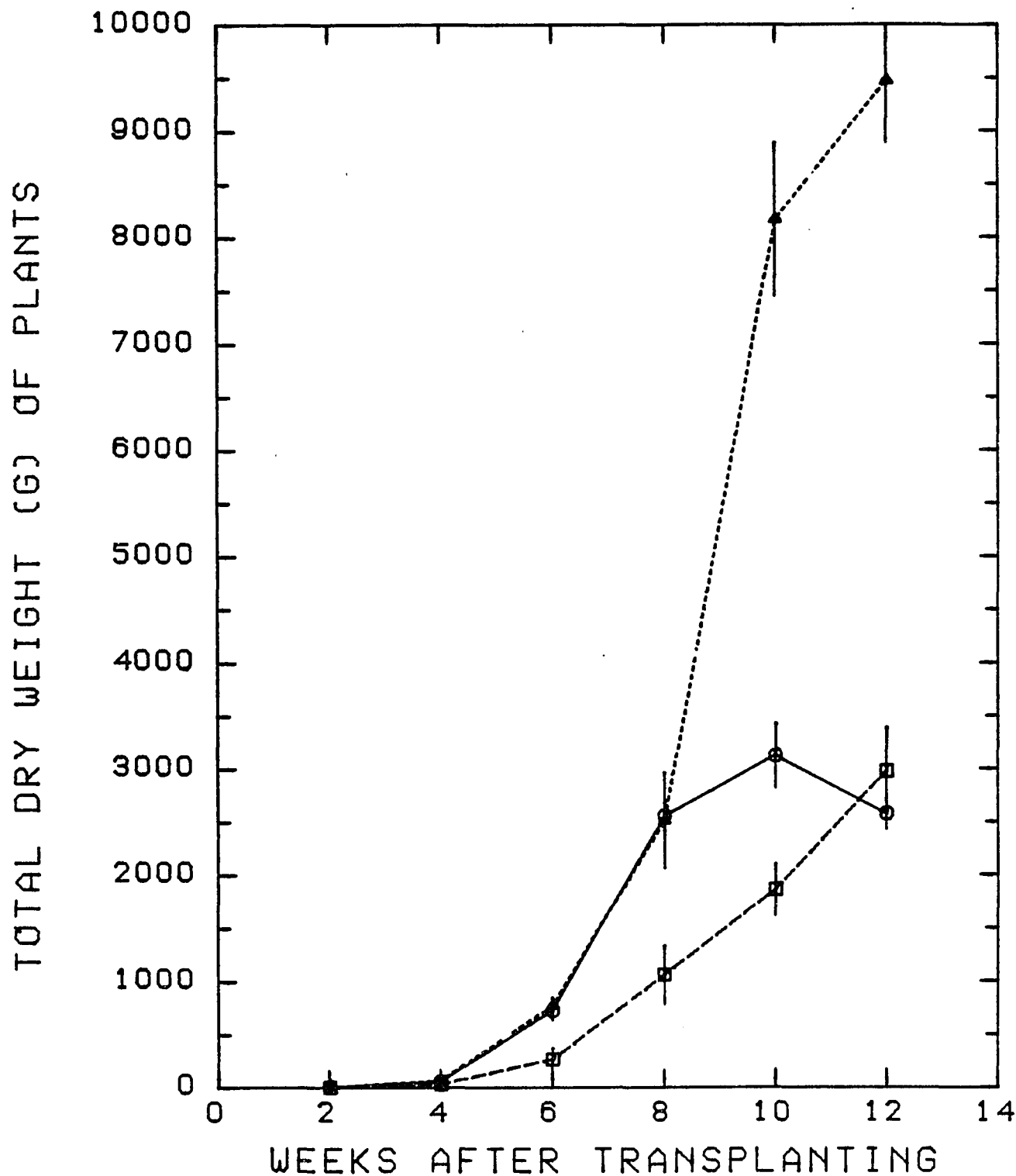


Figure 15: Total dry weight accumulation in 'Autumn Pride' (—), 'Blue Hubbard' (-----), and GA₃-treated 'Autumn Pride' (----) plants grown in the field in 1981. Values represent mean SE for 5 replicates.

leaves was consistently higher in 'Blue Hubbard' (Figure 16). After the eighth week, total biomass in leaves and stems of 'Autumn Pride' plants declined, whereas 'Blue Hubbard' plants exhibited growth of lateral vines.

Female flowering occurred 3 to 5 days earlier in 'Autumn Pride', as indicated by earlier accumulation of fruit dry weight in 'Autumn Pride' (Table 6). 'Autumn Pride' fruits became a strong sink within two weeks after fruit set, as shown by the decline in vegetative growth after the eighth week. At 8 weeks after transplanting, 'Autumn Pride' had deposited 49 per cent of its total dry weight into its fruits, compared to 35 per cent for 'Blue Hubbard'. By the tenth week, 'Autumn Pride' had 65 per cent of its total dry weight into its fruits, compared to 56 per cent for 'Blue Hubbard'. At the twelfth week, the values were 70 per cent for 'Autumn Pride' and 57 per cent for 'Blue Hubbard' (Figure 16).

At low density planting, vine plants averaged 4.4 ± 0.5 fruits per plant and bush plants averaged 1.8 ± 0.4 fruits per plant. 'Autumn Pride' plants set no more than two fruits per plant. The number of fruits set by GA_3 -treated bush plants varied between one and three, but averaged 2.0 ± 0.7 fruits per plant.

Analysis of Growth Rate

Specific Leaf Weight (SLW)

Leaves of 'Autumn Pride' had a higher SLW than leaves of 'Blue Hubbard' throughout the growing season, except at six weeks leaves of 'Blue Hubbard' had a high SLW (Table 7). SLW's closely paralleled the stage of plant development. SLW's were highest prior to fruit development then dropped significantly during rapid fruit development between the sixth and eighth weeks. SLW's in bush plants were high at 12 weeks, coinciding with the completion of fruit development.

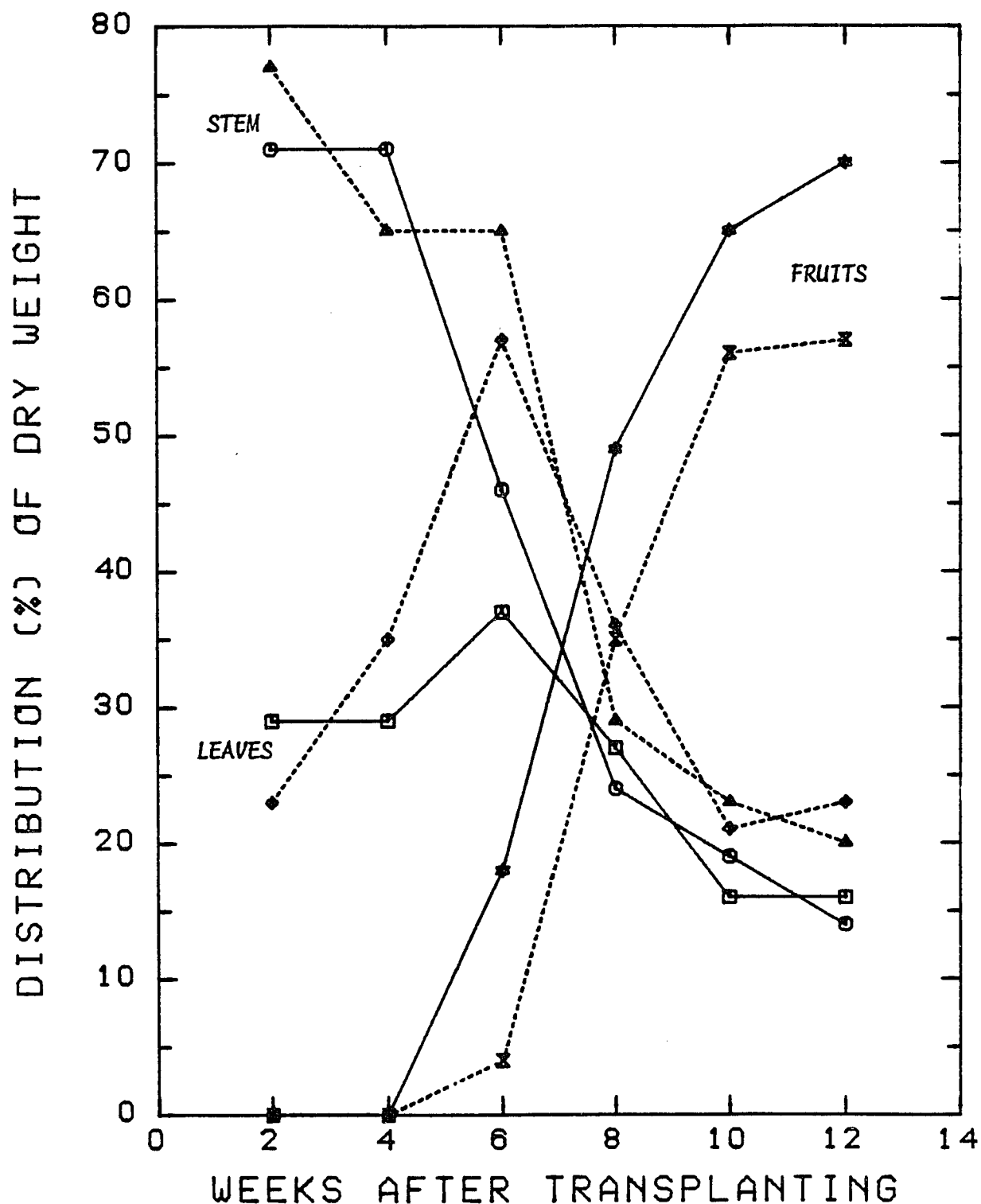


Figure 16: The partitioning of dry weight among leaves, stems, and fruits in 'Autumn Pride' (—) and 'Blue Hubbard' (-----) plants at low density planting in the field in 1981. Values represent means of determinations from 5 blocked replicates per treatment.

Table 6: The distribution of dry weight in stems, leaves, and fruits of 'Autumn Pride' (bush), 'Blue Hubbard' (vine), and GA₃-treated 'Autumn Pride' plants grown in the field in 1981.

Week	Organ	Plant Type or Plant Treatment		
		Bush (g)	Vine (g)	GA ₃ -treated (g)
2	Leaves	1.8	3.0	0.9
	Stems	0.7	0.9	0.7
	Fruits	0.0	0.0	0.0
	Total	2.5	3.9	1.6
4	Leaves	41.4	43.4	16.9
	Stems	17.2	23.2	17.2
	Fruits	0.2	0.0	0.0
	Total	58.6	66.6	33.1
6	Leaves	331	504	120
	Stems	265	437	115
	Fruits	129	31	32
	Total	725	972	267
8	Leaves	616	732	298
	Stems	689	912	472
	Fruits	1250	870	290
	Total	2555	2514	1060
10	Leaves	584	1886	504
	Stems	500	1688	412
	Fruits	2040	4600	940
	Total	3124	8171	1860
12	Leaves	368	1880	576
	Stems	414	2191	588
	Fruits	1790	5400	1810
	Total	2572	9471	2974

Table 7: Specific leaf weights (SLW = mg leaf cm⁻¹) of 'Autumn Pride' (bush), 'Blue Hubbard' (vine) and GA₃-treated 'Autumn Pride' plants during development in the field.

Treatment	Weeks After Transplanting				
	4	6	8	10	12
Bush	6.8	7.3	5.9	6.4	8.0
Vine	5.5	8.3	5.5	5.9	5.7
GA ₃ -treated	4.7	7.1	5.6	4.2	6.0

Table 8: Leaf area ratio (LAR = dm² g⁻¹ plant dry weight) of 'Autumn Pride' (bush), 'Blue Hubbard' (vine) and GA₃-treated 'Autumn Pride' plants during their development in the field.

Treatment	Weeks After Transplanting					
	2	4	6	8	10	12
Bush	1.06	1.04	0.62	0.41	0.29	0.17
Vine	1.39	1.19	0.79	0.54	0.39	0.35
GA ₃ -treated	1.26	1.09	0.63	0.51	0.64	0.31

Leaf Area Ratio (LAR)

The leaf area ratios (LAR's) for 'Autumn Pride' were consistently lower than those for 'Blue Hubbard' or the GA_3 -treated bush plants (Table 8). Thus, bush plants were more efficient than vine plants in the assimilation of dry matter per unit of leaf area.

Assimilation Rates

Rate of assimilation of dry matter is an effective criterion for the comparison of productivity. Cumulative net assimilation rates (NAR = g dry weight m^2 of leaf area d^{-1}) were consistently higher in 'Autumn Pride' than in 'Blue Hubbard' during the entire period of plant growth and development. Biweekly NAR determinations showed that bush plants had higher NAR's than vine plants until the NAR for bush plants peaked at the six to eight week period. Peak NAR for vine plants was at the eight to ten week period. The fact that biweekly NAR peaked at about $12.5 g m^2 d^{-1}$ for both strains indicated a similar growth potential for both types of plants during periods of rapid fruit development. The higher biweekly NAR for bush plants during the first eight weeks of growth, and consistently higher cumulative NAR of bush plants over vine plants (Table 9) showed that from early vegetative stages, bush plants were able to function at a higher efficiency than vine plants.

Harvest Index

'Autumn Pride' plants deposited 70 per cent of their total biomass into fruits, while 'Blue Hubbard' plants deposited only 57 per cent of their total biomass. This compares with harvest ratios of 73 per cent and 62 per cent for bush and vine plants, respectively, at the 1.2 x 1.5 m spacing in the yield trial in 1981. With increasing plant density, harvest ratios of 'Autumn Pride' increased from 73 per cent to 85 per

Table 9: Net assimilation rate (NAR) of plants grown at low density planting in the field in 1981.

A. Cumulative net assimilation rate (NAR = g dm^{-2} leaf area d^{-1})

Treatment	Weeks After Transplanting					
	2	4	6	8	10	12
Bush	6.77	3.44	3.81	4.34	5.29	6.81
Vine	5.14	3.01	3.03	3.34	3.62	3.42
GA ₃ -treated	5.68	3.28	3.76	3.53	2.23	3.79

B. Biweekly net assimilation rate (NAR = g dm^{-2} leaf area d^{-1})

Treatment	Weeks After Transplanting					
	2	4	6	8	10	12
Bush	2.86	7.67	10.50	12.44	4.82	-8.73 ^z
Vine	1.82	5.67	8.29	9.25	12.55	2.82
GA ₃ -treated	5.68	6.26	9.88	10.57	5.60	8.52

^zWith senescence of leaves, NAR may become negative, especially during fruit maturation.

cent at the highest plant density (Table 4).

The Anatomy of Winter Squash Leaves

Figure 17 shows cross sections of leaves of 'Autumn Pride' (bush) and 'Blue Hubbard' (vine) strains of winter squash. Two distinct layers of palisade parenchyma and a lower layer of spongy parenchyma were found in 'Autumn Pride'. In 'Blue Hubbard' the second layer of palisade parenchyma cells was less prominent than in bush plants. Both leaf structures were typical of C_3 plants, and the differences in leaf tissue composing each type are given in Table 10.

In both strains, the upper epidermis averaged about 20 μm thick, and the lower epidermis was 10 μm or less thick. The entire leaf sections of both 'Autumn Pride' and 'Blue Hubbard' were 200 ± 30 μm thick. Palisade parenchyma cells occupied an average of 74 per cent of the entire mesophyll in 'Autumn Pride', while the palisade parenchyma occupied about 52 per cent of the mesophyll in 'Blue Hubbard'.

Bundle sheaths surrounded large veins in the leaf, but the sheaths, when present, lacked chloroplasts, unlike those seen in C_4 species.

CO_2 Compensation Point of Winter Squash Leaves

Table 11 shows the compensation points of the bush and vine strains compared to values for corn, a C_4 plant, and beans, a C_3 plant. The leaves of 'Autumn Pride' consistently showed a lower compensation point (33 to 43 ppm) than the leaves of 'Blue Hubbard' (70 to 82 ppm). Values for the bush strain were similar to beans and considerably higher than that of corn (less than 10 ppm), a C_4 plant.

Translocation and Partitioning of ^{14}C -Sucrose

The short stem length of bush plants is a potential advantage for translocating assimilates out of source leaves into sink tissues, because

Table 10: The thickness of leaf tissues, lengths of tiers of palisade cells and per cent of leaf mesophyll occupied by different leaf tissues in fully-exposed mature leaves.

Leaf Tissue	'Autumn Pride'				'Blue Hubbard'			
	μm	\pm	SE	%	μm	\pm	SE	%
Palisade Parenchyma (Upper tier)	73	\pm	3 ^z	44	76	\pm	3 ^z	45
Palisade Parenchyma (Lower tier)	49	\pm	2	30	12	\pm	1	7
Spongy Parenchyma (Total)	43	\pm	2	26	80	\pm	3	48
TOTAL MESOPHYLL	165			100	168			100
Upper Epidermis	20	\pm	3	-	20	\pm	3	-
Lower Epidermis	10	\pm	2	-	10	\pm	2	-
TOTAL LEAF THICKNESS	195			-	198			-

^zEach value represents the mean of 10 measurements \pm SE (5 measurements/leaf, 2 leaves).



A. Cross section (10 μ m thick) of mature leaf of 'Blue Hubbard'



B. Cross section (10 μ m thick) of mature leaf of 'Autumn Pride'

Figure 17: Cross sections (10 μ m thick) of mature leaves of 'Blue Hubbard' (A, top) and 'Autumn Pride' (B, bottom) plants grown in full sunlight in the field.

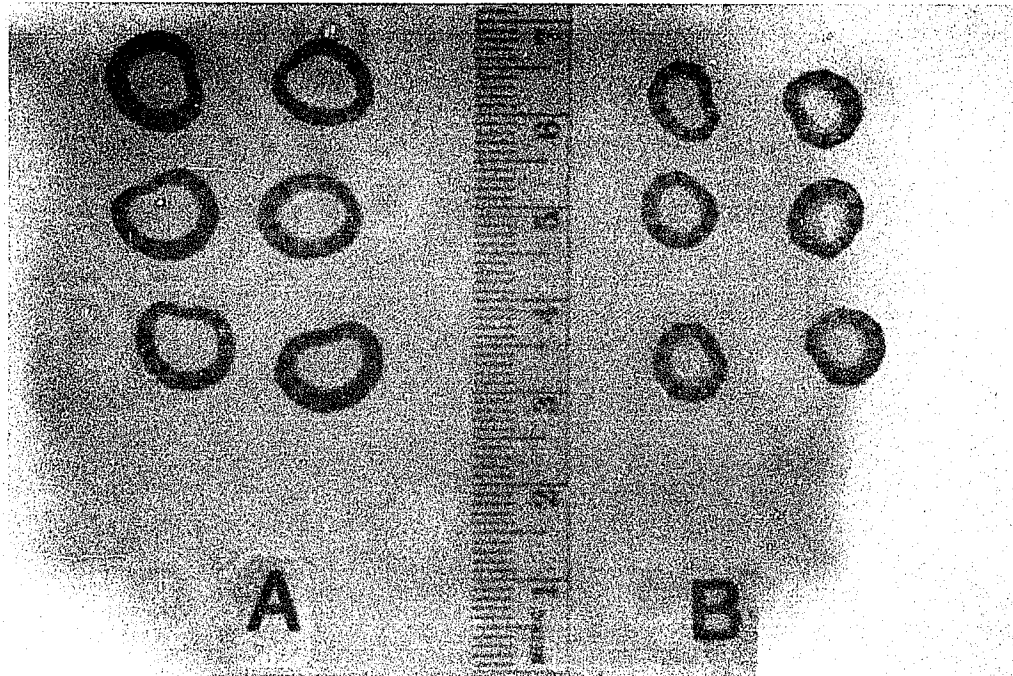
it makes all leaves more proximate to the apex, the root, and the fruit when it develops. In addition, stem tissues of bush ('Autumn Pride') plants had larger diameters and larger vascular bundles than stem tissues of vine ('Blue Hubbard') plants (Figure 18). Because of its larger vascular bundles, bush plants might be expected to show higher rates of mass transfer.

Preliminary attempts to monitor the movement of ^{14}C -sucrose into fruit sinks were difficult to replicate due to variation in fruiting dates and a high abortion rate of newly-formed fruits in the greenhouse. Because of these inconsistencies with reproductive sinks, vegetative sinks were used in studying the efficiency of translocation in bush and vine strains of winter squash.

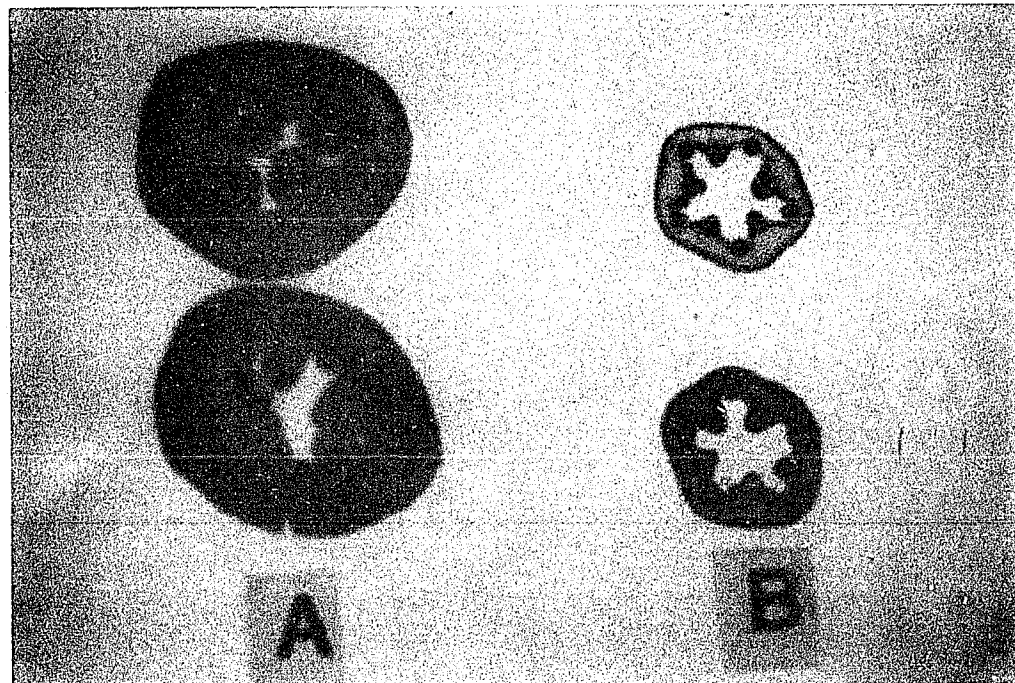
Figure 19 shows the activities (cpm) in 100 mg samples of different organs assayed 24 hours after feeding ^{14}C -sucrose to a source leaf (L) of plants grown in the greenhouse in the summer of 1981. A comparatively low activity (cpm) was found in the source leaves of bush plants after 24 hours. Considerably higher activity was present in petioles. In the sink tissues, the apex (A) contained higher counts of radioactivity than roots (R) after the 24-hour period.

In vine plants, high activity was found in the source leaf. The activity in the petiole was considerably lower. Of the sink tissues, the apex had a considerably higher activity than the root.

Although the apex (A) was the stronger sink in both 'Autumn Pride' and 'Blue Hubbard' during the summer experiment, a significantly higher activity (cpm) was consistently found in apices of 'Autumn Pride' plants in comparison to apices of 'Blue Hubbard' plants. Somewhat higher activities were found in root tissues of bush plants than in root tissues of



Top: Petioles of 'Autumn Pride' (A) and 'Blue Hubbard' (B)

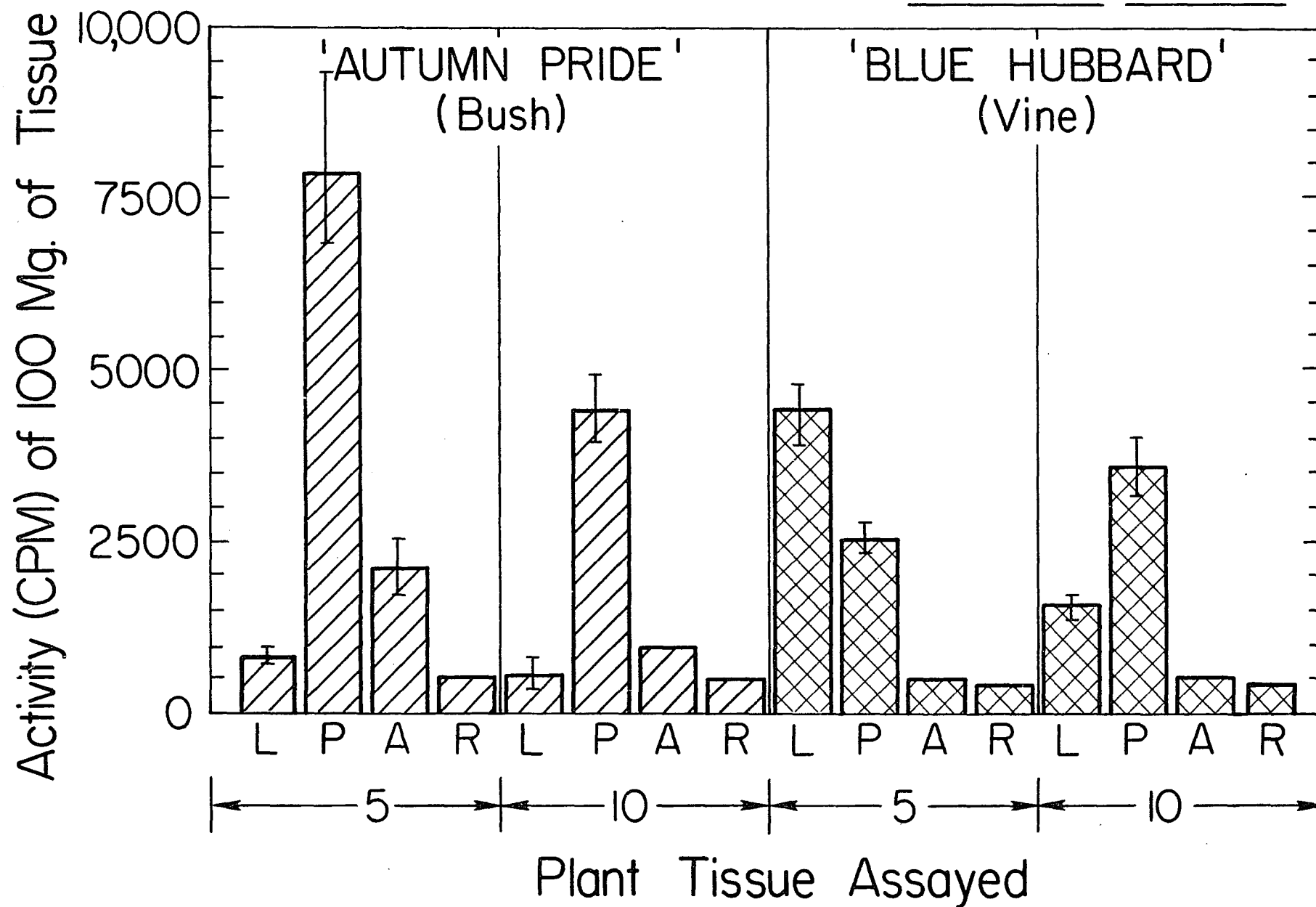


Bottom: Stems of 'Autumn Pride' (A) and 'Blue Hubbard' (B)

Figure 18: Cross sections of main stems (bottom) and petioles (top) of 'Autumn Pride' (A) and 'Blue Hubbard' (B) plants grown in the greenhouse during the summer of 1981.

Figure 19: The activity (cpm) found in 100 mg tissue samples of the fed leaf (L), the petiole (P) of the fed leaf, the apex (A), and the root (R) when either the fifth (5) or tenth (10) leaf of 'Autumn Pride' or 'Blue Hubbard' was fed 2×10^6 dpm of ^{14}C -sucrose. Plants were grown in the greenhouse in the summer of 1981.

^{14}C - Sucrose Translocation in Cucurbita Maxima



vine plants.

For plants grown in the greenhouse in winter of 1981, the activities (cpm) in 100 mg samples of different organs assayed were highest in the tissues of the source leaf (L) (Figure 20). Activities in petioles (P) were significantly lower. The roots (R) were consistently the predominant sink. Again bush ('Autumn Pride') plants were able to translocate more radioactivity into the root and apex than vine plants.

The activity (cpm) and total radioactivity (dpm) in each source and sink organ assayed are respectively given in Tables 11 and 12 for the summer experiment. The activities (cpm) and total radioactivities (dpm) assayed in the winter experiment are respectively given in Tables 13 and 14. In both plant types, more radioactivity was found in roots whose radioactivity source was the fifth leaf than in roots whose source was the tenth leaf, a more proximate position to the roots.

In total, a higher activity was recovered in sink organs of bush plants, but the proportion of recovered activity gives further indication of comparative translocation. Recovered activities in the fifth and tenth source leaves were 9.9 and 8.5 per cent, respectively, in the bush plant. In the vine plant, 65.0 and 32.7 per cent were found in the fifth and tenth leaves, respectively. The activities recovered in sink organs of the fifth and tenth leaves of bush plants were 64.3 and 44.4 per cent, respectively. This compares with only 19.4 and 22.3 per cent found in the respective sink tissues of vine plants.

Finally, the effect of position of source leaf and the distance between source leaf and sink organ on translocation is shown in Table 16. In the bush plant, the lamina of the fifth leaf averaged 17 cm away from its apex, and the lamina of the tenth leaf averaged 44 cm away. In the

Figure 20: The activity (cpm) found in 100 mg tissue samples of the fed leaf (L), the petiole (P) of the fed leaf, the plant apex (A), and the root (R) when either the fifth (5) or tenth (10) leaf of 'Autumn Pride' or 'Blue Hubbard' was fed 2×10^6 dpm of ^{14}C -sucrose. Plants were grown in the greenhouse in the winter of 1981.

^{14}C - Sucrose Translocation in Cucurbita Maxima

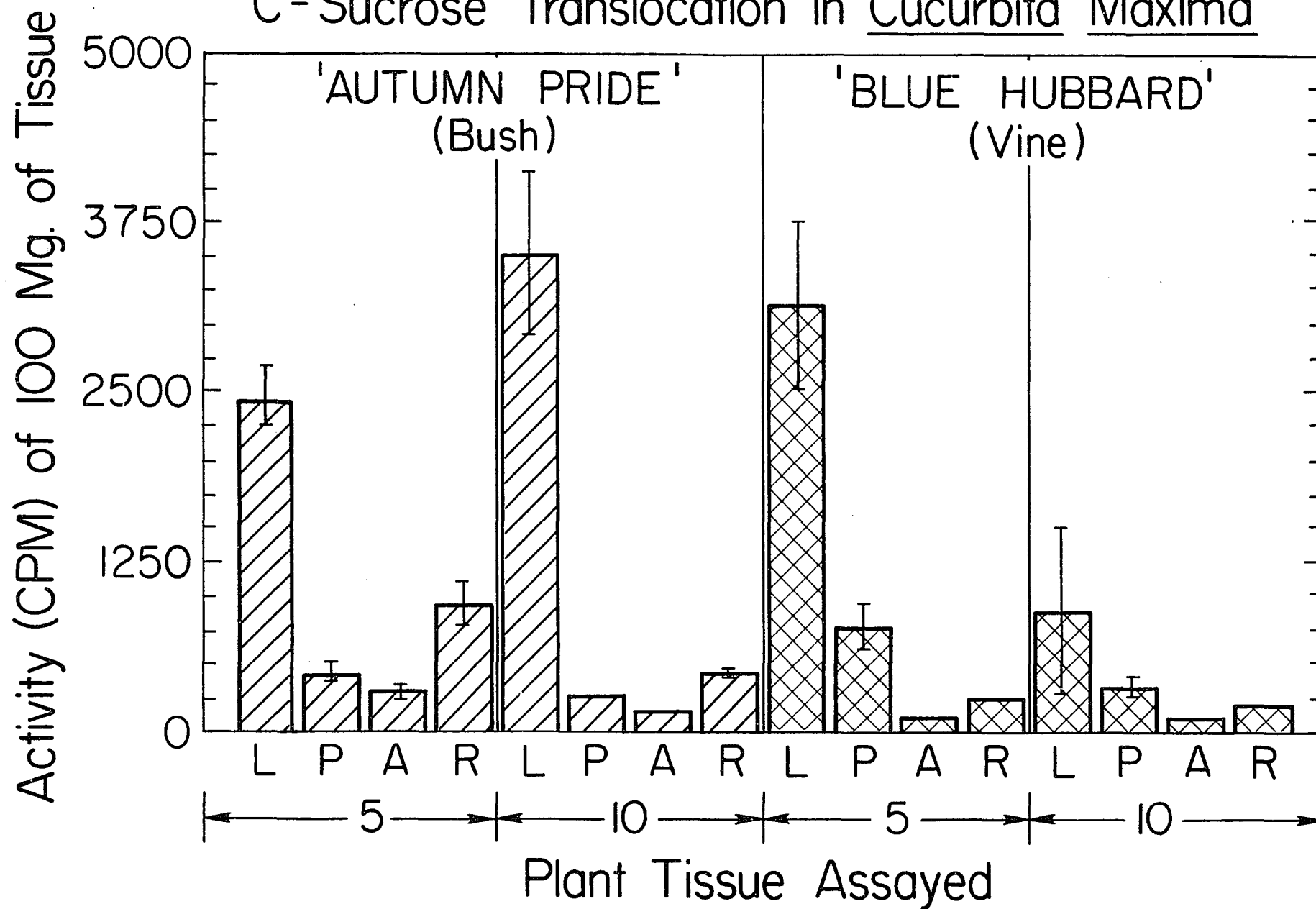


Table 11: Estimated CO₂ compensation points for 'Autumn Pride' (bush), and 'Blue Hubbard' (vine) squash leaves,² in comparison to CO₂ compensation points for corn and beans, as determined from pH changes in a 1×10^{-4} M sodium bicarbonate solution at 30°C. Initial pH of the NaHCO₃ solution was 6.99 in air.

Species	3-Hr Light Period		18-Hr Light Period		Dark Control	
	pH	ppm CO ₂	pH	ppm CO ₂	pH	ppm CO ₂
<u>Phaseolus vulgaris</u> (Beans)	8.15 \pm 0.06 ^z	43	8.18 \pm 0.10 ^z	43	6.29 \pm 0.10 ^z	300
<u>Zea mays</u> (Corn)	8.92 \pm 0.05	5	8.89 \pm 0.06	5	6.71 \pm 0.16	300
<u>Cucurbita maxima</u>						
'Blue Hubbard'	7.95 \pm 0.06	70	7.92 \pm 0.09	82	6.19 \pm 0.17	300
'Autumn Pride'	8.28 \pm 0.03	33	8.17 \pm 0.10	43	6.71 \pm 0.10	300

^zEach value represents the mean of 3 measurements \pm standard error.

Table 12: Radioactivity (cpm) and per cent of radioactivity recovered in squash organs sampled 24 hours after feeding 2×10^6 dpm ^{14}C -sucrose to either the fifth or tenth leaf of 'Autumn Pride' or 'Blue Hubbard' in the summer 1981 greenhouse experiment. (Radioactivity = Activity in 100 mg x 10 x the number of grams making up organ sampled).

Organ Assayed	'Autumn Pride'				'Blue Hubbard'			
	Leaf-5		Leaf-10		Leaf-5		Leaf-10	
	cpm	%	cpm	%	cpm	%	cpm	%
Fed Leaf	18,923 ^z	9.9	8,262 ^z	8.5	30,095 ^z	65.0	12,294 ^z	32.7
Petiole	49,125	25.8	45,206	46.7	7,216	15.6	16,884	45.0
Apex	115,626	60.7	37,419	38.6	5,570	12.0	5,232	13.9
Root	6,862	3.6	5,967	6.2	3,425	7.4	3,149	8.4
TOTAL	190,536	100.0	96,854	100.0	46,306	100.0	37,559	100.0

^zEach value is a mean of 5 replicates

Table 13: Total radioactivity (dpm) and per cent of total radioactivity recovered in squash organs sampled 24 hours after feeding 2×10^6 dpm ^{14}C -sucrose to either the fifth or tenth leaf of 'Autumn Pride' or 'Blue Hubbard' in the summer 1981 greenhouse experiment. (Radioactivity (dpm) is determined from the variable degree of quenching in different tissues.)

Organ Assayed	'Autumn Pride'				'Blue Hubbard'			
	Leaf-5		Leaf-10		Leaf-5		Leaf-10	
	dpm	%	dpm	%	dpm	%	dpm	%
Fed Leaf	450,548	23.4	165,240	12.0	1,433,095	86.5	491,760	53.7
Petiole	405,992	21.0	475,852	34.5	68,724	4.1	186,840	18.4
Apex	947,754	49.2	668,196	48.4	94,409	5.7	209,280	22.9
Root	122,536	6.4	70,200	5.1	61,161	3.7	45,638	5.0
TOTAL	1,926,830	100.0	1,379,488	100.0	1,657,389	100.0	915,519	100.0

Table 14: Radioactivity (cpm) and per cent of radioactivity recovered in squash organs sampled 24 hours after feeding 2×10^6 dpm ^{14}C -sucrose to either the fifth or tenth leaf of 'Autumn Pride' or 'Blue Hubbard' in the winter 1981 greenhouse experiment. (Radioactivity = Activity in 100 mg \times 10 \times the number of grams making up organ sampled).

Organ Assayed	'Autumn Pride'				'Blue Hubbard'			
	Leaf-5		Leaf-10		Leaf-5		Leaf-10	
	cpm	%	cpm	%	cpm	%	cpm	%
Fed Leaf	19,595	82.0	29,288	94.3	11,243	89.8	19,440	96.2
Petiole	1,306	5.5	718	2.3	704	5.6	333	1.6
Apex	1,666	7.0	389	1.3	309	2.5	217	1.1
Root	1,318	5.5	665	2.1	262	2.1	216	1.1
TOTAL	23,885	100.0	31,060	100.0	12,518	100.0	20,206	100.0

^zEach value is a mean of 4 replicates.

Table 15: Total radioactivity (dpm) and per cent of total radioactivity recovered in squash organs sampled 24 hours after feeding 2×10^6 dpm ^{14}C -sucrose to either the fifth or tenth leaf of 'Autumn Pride' or 'Blue Hubbard' in the winter 1981 greenhouse experiment. (Radioactivity (dpm) is determined from the variable degree of quenching in different tissues.)

Organ Assayed	'Autumn Pride'				'Blue Hubbard'			
	Leaf-5		Leaf-10		Leaf-5		Leaf-10	
	dpm	%	dpm	%	dpm	%	dpm	%
Fed Leaf	466,548	91.6	585,760	96.0	535,381	97.0	777,600	98.0
Petiole	10,793	2.1	7,558	1.2	6,863	1.2	3,330	0.4
Apex	13,655	2.7	6,946	1.2	5,237	1.1	8,680	1.1
Root	18,563	3.6	9,637	1.6	4,678	0.8	3,875	0.5
TOTAL	509,559	100.0	609,901	100.0	552,159	100.0	793,467	100.0

Table 16: The effect of position of source leaf and distance between source leaf and sink organ on the recovery of radioactivity (cpm) in sink organs of bush and vine strains of winter squash in summer, 1981.

Factor	'Autumn Pride'		'Blue Hubbard'	
	Leaf-5	Leaf-10	Leaf-5	Leaf-10
APEX (SINK)				
Petiole length (cm)	12	31	7	12
Stem length (cm) ^z	5	13	40	128
Total distance (cm)	17	44	47	140
Activity (cpm)	115,626	37,419	5,270	5,232
ROOT (SINK)				
Petiole length (cm)	12	31	7	12
Stem length (cm) ^y	10	6	165	112
Total distance (cm)	22	37	172	124
Activity (cpm)	6,862	5,967	3,425	3,149

^zDistance between the leaf node and the apex on the main stem.

^yDistance between the leaf node and the root on the main stem.

vine plant, the average distances between the lamina of the fifth leaf and the apex was 47 cm, and 140 cm for the tenth leaf. The distances between the source leaves and root sink showed similar variation with leaf position. The distance traversed between source and sink was significantly shorter for bush plants than for vine plants.

These results are further indication that mass transfer is higher in bush ('Autumn Pride') plants than in vine ('Blue Hubbard') plants.

V. DISCUSSION

Plant Architecture

The bush 'Autumn Pride' plant is an architectural advance over the vining 'Blue Hubbard' plant in terms of plant productivity and crop management. In addition to being a brachytic dwarf, a primary feature is its erect and upright habit of growth. 'Autumn Pride' plants hold their leaves in a canopy much higher than that of vining 'Blue Hubbard' plants because of longer petioles borne on the stem at least several centimeters above the ground. The dense planting pattern of 'Autumn Pride' plants causes its leaves to assume a funnel morphology. This exposes a larger leaf area to incident light and permits light penetration into the lower canopy. Furthermore, petioles of bush plants exhibited greater elongation with increase in plant density. Duncan (1975) reported a similar increase in stem elongation in corn with increase in population density.

The morphology of the bush plant contrasts sharply with the more prostrate trailing vines of 'Blue Hubbard', having a lower canopy height. Petioles are a major structure which contribute to canopy height in winter squash, but in vine plants the leaves were borne at ground level on prostrate, not erect, stems. Secondly, vine plants bear tendrils in their leaf axils, and some petioles and many leaves in the path of the elongating stems were pulled down by clinging tendrils. The resultant aggregations of mutually-shading stems and leaves were abundant in stands of vine plants along with contrasting areas of sparsely-covered soil.

Although actual experimental data illustrating a relationship be-

tween leaf and canopy architecture and plant yield are difficult to find, Loomis and Williams (1969) discussed the contribution of vertical distribution of leaves to light interception. They noted that the hypothesis that erect leaves confer tolerance to crowding is widely accepted. With increased plant density, yields are known to increase, providing indirect evidence of benefits.

Leaf Production

Eight weeks after transplanting, 'Blue Hubbard' plants had an average of more than two times the number of leaves because of its multiple branching habit. Both secondary and tertiary laterals are produced by vine plants, resulting in a web of stems and a tremendous capacity for leaf production.

The advantage of vine plants in leaf production is offset by the adaptability of bush plants to high density planting. Thus bush plants at high density planting exhibited rapid early canopy development, as indicated by higher LAI's in 'Autumn Pride' than in 'Blue Hubbard' during the first weeks of growth.

Leaf area development for 'Blue Hubbard' was at a slower rate during the first few weeks due to the formation of branch stems, but beginning in the fourth week in the field, leaf area increased rapidly. Leaf area duration (LAD) was greater for 'Blue Hubbard' due to its continued vegetative growth.

Indeterminate tomato cultivars develop a large leaf area similar to 'Blue Hubbard'. This is considered undesirable because it is associated with scattered fruit set which interferes with mechanical harvesting (Hewitt and Stevens, 1981). It is coincident that 'Blue Hubbard' and other vining squash plants are also known for scattered fruit set.

Leaf Area Index and Yield

In general, optimum leaf area indices (LAI's) range between 4 and 8 (Watson, 1952). Corn produced its best yields at LAI's between 4.0 and 7.5 (Duncan, 1958). Moorby and Milthorpe (1975) reported peak LAI's between 4.0 and 4.5 in potato, and for sugar beet, a peak LAI of 6.0 was obtained by computer simulation for optimum crop development (Fick et al., 1963).

For 'Autumn Pride', the highest LAI's were 6.0 at the 30 cm spacing at six weeks after transplanting. At the same date, the LAI's for 'Autumn Pride' and 'Blue Hubbard' at 120 cm in-row spacing were 2.8 and 3.5, respectively. LAI's for 'Blue Hubbard' reached 9.2 at 7 weeks from transplanting. Such a high index may be a necessary balance for achieving rapid canopy cover at the expense of excessive mutual shading of leaves late in the growing season.

Among 'Autumn Pride' plants, fresh weight yields closely paralleled LAI's, and at 30 cm and 60 cm in-row spacings, yields were significantly higher than the yield of 'Blue Hubbard'.

Fruit Characteristics and Yield

There was significant reduction in per cent dry matter with increase in plant density, confirming preliminary results in 1980. With this consideration of biomass production, only the highest plant density of 'Autumn Pride' out-yielded 'Blue Hubbard' at its presumed near optimum density. This was because 'Blue Hubbard' fruits had a higher dry matter content than 'Autumn Pride' fruits. Stevens (1976) suggested that determinate tomato cultivars may have lower solid content because of their lower leaf area ratios, and Hewitt and Stevens (1981) showed that indeterminate plants produced fruits with higher solid content (per cent dry

weight). This is evidently the case with 'Autumn Pride', which exhibits a determinate-like growth habit following fruit set and development (Zack and Loy, 1981).

A reduction in fruit size with increase in plant density occurred in 'Autumn Pride'. Within any plant density though, fruits produced by 'Autumn Pride' plants were very uniform in size. Duncan (1958) reported a reduction in ear size in maize with increase in plant density. Similarly, Moorby and Milthorpe (1975) reported that with increase in stem density, there is a decrease in mean potato tuber size at harvest. There are similar reports for most crops, and Fick et al. (1975) reported that for sugar beet, each plant achieves much less than its potential root size because of high density planting under field conditions.

The higher dry weight yield for 'Autumn Pride' at its highest plant density emphasizes that the benefits of the bush habit are accrued at high plant populations. Unfortunately, the 0.3 x 1.2 m spacing cannot be recommended as the best plant spacing, because only one between-row spacing was used to evaluate the effect of plant density, and because many fruits produced at this spacing were not marketable. Square plantings of 0.6 x 0.6 m or 0.9 x 0.9 m may be more conducive to higher yields, but larger between-row spacings, as used in these trials, are more amenable to mechanized culture.

Dry Matter Partitioning and Yield

The similarity in total dry weights of bush and vine plants, both in the greenhouse and in the field, is very significant. These data showed that the most critical difference in productivity between bush and vine crops was not the total mass accumulated, but the strategy of distributing biomass firstly into photosynthetically active tissues, and

then into the economic organ of the plant.

Dry matter in 'Autumn Pride' was assimilated into vegetative structures during early plant development, then unilaterally into fruit growth and development. When the 'Autumn Pride' plant was channelling its entire assimilates into its fruits, the vine 'Blue Hubbard' plant was still partitioning its assimilates into both vegetative tissues and fruits. Rapid development of leaf area, and then the partitioning of dry matter into the fruit sink is a characteristic of modern crop plants (Evans and Wardlaw, 1976; Gifford and Evans, 1981).

Greenhouse studies showed that an additional partitioning strategy in the bush plant is the development of a larger main root. Unlike 'Blue Hubbard' plants which form roots at stem nodes, the main roots of 'Autumn Pride' were the only roots supporting the plant during its development. The recorded decline in root dry weight at the beginning of flower production is an important physiological index of change in the pattern of assimilate distribution, and each plant treatment ('Autumn Pride', 'Blue Hubbard', or GA₃-treated 'Autumn Pride' plants) exhibited this phenomenon. Similar reductions in root dry weight have been recorded at heading in both temperate and sub-tropical cereals (Welbank and Williams, 1968; Menzel and Barber, 1974; Murata and Matsushima, 1975).

The harvest ratios determined for plants in the 1981 plant density and yield trial showed that while only 66 per cent of the total fresh weight of the 'Blue Hubbard' plant was partitioned into its fruits, between 75 and 85 per cent was partitioned into fruits of 'Autumn Pride'. Harvest ratios are a less accurate measure of partitioning, for they are based on fresh weight data. However, they are good indicators of the

distribution of biomass between vegetative and reproductive organs which make up biological yield.

The harvest index of 70 per cent for 'Autumn Pride' and 57 per cent for 'Blue Hubbard' at low plant density confirm that the fruit of 'Autumn Pride' is a stronger sink than fruits of 'Blue Hubbard' during their plant development. These harvest indices are comparable to those of determinate and indeterminate tomato cultivars, which were about 70 per cent and 53 per cent, respectively (Hewitt and Stevens, 1981), but higher than those of many other crops. Kahn et al. (1981) obtained harvest indices of between 55.8 and 58.9 per cent for black beans (Phaseolus vulgaris). Harvest indices of cereals, which have improved from about 40 per cent to a new maximum of around 55 per cent with improvement in cereal yields (Donald and Hamblin, 1976; Gifford and Evans, 1981), are still comparatively low.

Analysis of Growth Rates

Some of the most significant developmental differences between 'Autumn Pride' and 'Blue Hubbard' were noted in growth analysis of total biomass in above-ground organs in field-grown plants and total plant biomass in the greenhouse-grown plants. Leaf canopy development, specific leaf weight (SLW) and cumulative net assimilation rates (NAR) were significantly higher for 'Autumn Pride' than for 'Blue Hubbard'. A consequence of these features was the higher dry weight production per unit of leaf area of 'Autumn Pride'. This suggests a greater efficiency of the photosynthetic apparatus of the bush 'Autumn Pride' plant.

The use of GA_3 to produce a vine phenocopy of 'Autumn Pride' plants provided additional evidence that growth analysis differences between 'Autumn Pride' and 'Blue Hubbard' were not merely cultivar differences,

but were differences mainly attributable to their different genetically-determined growth habits. The GA_3 -treated 'Autumn Pride' plants were initially spindly due to supra-optimal levels of exogenously applied GA_3 . After several weeks of growth, GA_3 -treated plants became more robust, and their morphological appearance approached that of the vine plants. The GA_3 -induced vine plants in the greenhouse tended to mimic the developmental pattern of the 'Blue Hubbard' strain, producing longer main stems, more leaves, higher LAR's, lower SLW's and fewer roots.

In the field, GA_3 -treated plants produced 1 to 3 fruits per plant unlike 'Autumn Pride' plants which never produced more than 2 fruits per plant, and like 'Blue Hubbard' plants which averaged more than 4 fruits per plant. Stems of GA_3 -treated bush plants exhibited the trailing habit of growth and initiated adventitious roots at the nodes, and plants had more leaves, a higher LAR, and a lower SLW, as in 'Blue Hubbard'. The most unexpected feature was the abundance of tendrils in leaf axils of GA_3 -treated 'Autumn Pride' plants throughout the development in the field. Moreover, they were found on bush plants displaying renewed semi-vining growth following fruit abortion in bush 'Autumn Pride' plants. Whitaker and Davis (1962) reported that tendrils are absent in bush plants.

Efficiency of the Photosynthetic Apparatus

The CO_2 compensation points of 'Autumn Pride' and 'Blue Hubbard' plants were well in the range for C_3 plants, but the lower CO_2 compensation point for 'Autumn Pride' indicated that its improved assimilation rate may be in part due to a higher net photosynthetic rate.

The difference in CO_2 compensation point between these two winter squash strains is a rare occurrence among C_3 crop cultivars. Moss et al.

(1969) found only one wheat variety with a slightly lower CO_2 compensation point in his examination of 100 cultivars. Cannell et al. (1969) found no difference among 44 soybean genotypes. The CO_2 compensation point of 'Autumn Pride' was quite similar to that of the bean plant (Phaseolus vulgaris), which is regarded as a typical sun plant (Bohning and Burnside, 1956).

Several microscopic examinations of cross sections of leaves of 'Autumn Pride' and 'Blue Hubbard' did not reveal any consistent differences in leaf thickness, but 'Autumn Pride' leaves had a more completely developed second palisade layer, as compared to 'Blue Hubbard'. The predominance of palisade parenchyma cells in the mesophyll of 'Autumn Pride' leaves may have initially developed as an ontogenic response to the availability of light on both abaxial and adaxial surfaces of the leaf, due to the high leaf angle of the bush plant, as seen in its funnel-shaped leaves. Dengler (1981) grew sunflower plants in full sunlight or shade and found that although sun leaves were thicker due to more elongated palisade cells, the relative proportion between palisade and spongy mesophyll cells did not change significantly. The mesophyll of shaded leaves were reported to have a greater proportion of intercellular space, though.

Between 'Autumn Pride' and 'Blue Hubbard', the fact that leaf thickness was not found to be significantly different and that the proportion of the leaf occupied by palisade parenchyma was found to be significantly higher for 'Autumn Pride' indicate that the differences between leaf anatomy of 'Autumn Pride' and 'Blue Hubbard' are characteristic of the strains, and not mere ontogenic differences caused by differences in light availability.

With the development of two expanded layers of palisade cells and a reduced thickness of the spongy mesophyll, bush leaves exhibited a more compact anatomy. This compactness of leaf tissues may account for the higher specific leaf weight found in 'Autumn Pride' leaves.

Specific leaf weight has been strongly correlated with higher net assimilation rates and greater photosynthetic efficiency (Wallace et al., 1972). Nobel (1974) discussed how a larger volume of palisade cells adds greater surface area to the internal photosynthetic structure and how this may be related to increased photosynthetic rates.

Bjorkman (1963) and several other workers have reported greater specific leaf weight in sun than in shade plants. Most reports of differences in specific leaf weight have been attributed to differences in leaf thickness (Wallace et al., 1972; Boardman, 1977). Results of Holgrem (1968) and Nobel et al. (1975) suggest that mesophyll cell area may explain the higher photosynthetic rates observed in sun leaves. The larger cell surface area means greater exchange and greater activity for these cells and their constituent chlorophyll molecules.

Translocation and Yield Improvement

Although ^{14}C -sucrose was used as the radioactive source, Webb and Gorham (1964, 1965) and Webb and Burley (1964) showed that stachyose with a trace of raffinose and sucrose were the principal compounds translocated to all parts of the Cucurbita melopepo plant, except to mature leaves. These observations on Cucurbita translocation have also been reported and confirmed by other reserchers (Zimmermann, 1957; Zeigler, 1975). Because sucrose is a natural precursor to stachyose (Gander, 1976), the use of ^{14}C -sucrose rather than labelled stachyose should not affect the interpretation of the translocation studies. Within the plant ^{14}C -sucrose should be readily converted to stachyose.

Mass transfer per unit area of phloem (SMT) in C. maxima has been reported to be between 4.5 and 4.8 g cm⁻² hr⁻¹ (Crafts and Lorenz, 1944). With stem tissues of bush ('Autumn Pride') plants having a larger cross-sectional area (Fig. 17), the capacity for mass transfer should be significantly larger than in 'Blue Hubbard'. The higher counts found in the apex and root sink tissues of bush as compared to vine plants following application of ¹⁴C-sucrose to leaves may in part be related to the greater phloem area of bush plants.

A second factor influencing mass transfer is the proximity of the sink to source leaves. Although petioles of 'Autumn Pride' plants are significantly longer than those of 'Blue Hubbard', leaves of 'Autumn Pride' plants are more proximal to their sinks. With approximately 100 'Autumn Pride' leaves separated on a 50 cm main stem compared to about 300 'Blue Hubbard' leaves separated on a 600 cm main stem under field conditions, 'Blue Hubbard' assimilates must be transferred an average of four times the distance to a fruit sink.

The effect of sink proximity on mass transfer has been studied in numerous crops. Mason and Maskell (1928) studied it in Phaseolus beans, and Webb and Gorham (1964), among others have studied it in Cucurbita. Canny (1973) reviewed these and numerous other studies and concluded that "high rates of transport can be achieved only over short distances; over long distances only low rates are possible." Canny (1975) reported that the plot of specific mass transfer (SMT) between source and sink would be a hyperbola, and that SMT beyond distances of "50 cm or so" would be slow. The shorter distance between source and sink is an advantageous characteristic of 'Autumn Pride'. This was vividly demonstrated in bush plants where the more proximate apex (17 cm away) received almost four

times the activity of the more distal apex (44 cm away). In contrast, mass transfer in vine plants was quite low.

Proximity between source and sink is an important factor, but in addition, the relative strength of sinks can vary, depending on sink characteristics and environmental conditions. Proportionally, there was a higher transport out of source leaves in summer-grown plants than in winter-grown plants. The major cause was probable the difference in light intensity between the two seasons. Ryle et al. (1980) obtained similar results when they showed that with increasing light intensity the supply of labelled assimilates to stolons of white clover increased. The total effect of a larger export from source leaves during summer may be an interaction between light and temperature. Greenhouse temperatures in the winter were significantly lower than those of the summer despite winter heating of the greenhouse. There is a strong positive correlation between temperature increase and translocation at temperatures between 0°C and 30°C (Canny, 1973; 1975).

The apex was a stronger sink in the summer, but the root was a more effective sink in the winter experiment. Several factors have been reported to govern the distribution of assimilates. Shibles et al. (1975) reported that soil temperatures of 22°C to 27°C seem most favorable to root growth in soybeans. Root growth in wheat and other cereals exceeds shoot growth at low temperatures (Evans et al., 1975; Evans and Wardlaw, 1976). Results of Guy et al. (1981) showed significantly larger storage of labelled starch in roots of seedling oranges at 10°C than at 25°C. With Vicia faba Crompton et al. (1981) found that before any flowers set, most of the radioactivity from all expanded leaves moved downwards to the roots and the stem below the treated leaf.

The Productivity of Winter Squash

The productivity of winter squash (Cucurbita maxima Duch.) is quite high, considering that its entire biomass is produced within 90 to 120 days. Whitaker and Davis (1962) wrote that winter squash is the best producer among the cucurbits, and with data obtained in these experiments, the productivity of winter squash can be compared to other crops, including non-vegetable crops.

Zelitch (1971) calculated the average productivity of several leafy crops in the United States. The crops were selected to provide estimates which were "almost entirely dependent on the total quantity of CO_2 assimilated less that lost by respiration." Maize silage, sorghum silage, and sugar cane, all C_4 crops, were determined to have crop growth rates (CGR's) of 50, 45, and 50 $\text{g dry weight m}^{-2} \text{ week}^{-1}$, respectively. Spinach, tobacco (leaf and stem), and "hay", all C_3 crops, were determined to have CGR's of 11, 25, and 16 $\text{g m}^{-2} \text{ wk}^{-1}$.

The question may be asked again: How does winter squash compare? Using the harvest indices obtained in the 1981 trial, dry matter yields can be determined, and the average productivity of winter squash can be estimated. On this basis, Tables 17 and 18 provide determinations of productivity of winter squash.

The growth periods of these crops were two weeks in the greenhouse plus twelve weeks in the field, making a total of 14 weeks. Because maximum dry weights of fruits of 'Autumn Pride' plants were obtained at 10 weeks in the field at low density planting, it may be argued that the season for 'Autumn Pride' is only 12 weeks. Thus, CGR's are also calculated for a 12 week period for 'Autumn Pride'.

Crop growth rates were between 31 and 38 $\text{g m}^{-2} \text{ wk}^{-1}$ for 'Autumn

Table 17: Crop yields and crop growth rates (CGR's) for 'Autumn Pride', at four plant densities, and for 'Blue Hubbard', at its near optimum plant density, in 1981.

Estimated Plant Density (pl/ha)	Market Yield (kg fresh wt/ha)	Dry Weight (kg dry wt/ha)	Growing Season (Weeks)	Crop Growth Rate (g/m ² /week)
'Autumn Pride'				
22,222	74,800	5,302	14 (12) ^y	38 (44) ^z
11,111	61,500	4,551	14 (12)	33 (38)
7,407	55,300	4,313	14 (12)	31 (36)
5,556	52,200	4,594	14 (12)	33 (38)
'Blue Hubbard'				
5,556	50,700	4,867	14	35

^zCalculated from per cent dry weight values obtained from 3 blocks, 4 fruits per plot.

^yActual growing season based on period during which dry weight increased.

Table 18: Biological yields and crop growth rates (CGR's) for 'Autumn Pride', at four plant densities, and for 'Blue Hubbard', at its near optimum plant density, in 1981.

Estimated Plant Density	Mean Fr. Wt. Biological Yield	Mean Dry Wt. Biological Yield	Estimated Growing Season	Biological Crop Growth Rate
(pl/ha)	(kg/ha)	(kg/ha)	(Weeks)	(g/m ² /wk)
'Autumn Pride'				
22,222	88,560	7,574 ^z	14 (12) ^y	54 (63) ^x
11,111	74,784	6,501	14 (12)	46 (54)
7,407	71,356	6,161	14 (12)	44 (51)
5,556	70,560	6,563	14 (12)	47 (55)
'Blue Hubbard'				
5,556	79,150	8,539	14	61

^zBased on the 70 per cent and 57 per cent harvest indices obtained for 'Autumn Pride' and 'Blue Hubbard', respectively, at low density planting.

^yActual growing season, based on the period during which dry weight increased.

^xValues based on actual length (12 weeks) of the growing season.

Pride' and $35 \text{ g m}^{-2} \text{ wk}^{-1}$ for 'Blue Hubbard' for the 14-week period. With the 12-week season, crop growth rate was as high as $44 \text{ g m}^{-2} \text{ wk}^{-1}$ in 'Autumn Pride'. The estimated biological crop growth rates were $61 \text{ g m}^{-2} \text{ wk}^{-1}$ for 'Blue Hubbard' and between 47 and $54 \text{ g m}^{-2} \text{ wk}^{-1}$ for 'Autumn Pride' in the 14-week season. For the 12-week season, biological crop growth rates for 'Autumn Pride' were between $51 \text{ g m}^{-2} \text{ wk}^{-1}$ and $63 \text{ g m}^{-2} \text{ wk}^{-1}$. Thus at near optimum planting densities, the bush and vine plants had similar biological crop growth rates (CGR's), but the bush plant exhibited higher maximum yields because of a higher harvest index.

The values reported here for 'Autumn Pride' are under small research plot conditions and may be high, but they emphasize the high productivity attainable in winter squash.

VI. CONCLUSION

The patterns of growth and development in hush and vine strains were distinctly different. 'Blue Hubbard' plants exhibited more elongated main stem and branch stems and more rapid production of leaves than 'Autumn Pride' plants which exhibited extremely short internodes and a thickened main stem. In both field-grown and greenhouse-grown plants, 'Blue Hubbard' and 'Autumn Pride' plants accumulated similar amounts of dry matter over the first eight weeks of growth. Bush plants partitioned more dry weight into leaves and roots, and less into stems. Fruit set was 3 to 5 days earlier in 'Autumn Pride', and fruit development began at about six weeks after transplanting into the field. At eight weeks in the field, vegetative development in bush plants ceased, as assimilates were partitioned almost exclusively into the developing fruit. In contrast, 'Blue Hubbard' continuously partitioned dry weight between vegetative and reproductive tissues. Fruits became a stronger sink beginning at the eighth week after transplanting, but leaf and stem dry weight formed a large portion of the entire biomass produced.

Maximum biological productivity of bush and vine cultivars were as high as 7574 and 8539 kg ha⁻¹, respectively. Dry weight fruit yields were as high as 4867 kg ha⁻¹ for 'Blue Hubbard' and 5302 kg ha⁻¹ for 'Autumn Pride', the greater productivity of 'Autumn Pride' being due to a higher harvest index. 'Autumn Pride' reached its peak yield at the highest plant density.

Morphological attributes contributing to the high yield and quality of bush winter squash were the early development of a high and complete

leaf canopy, the high angular exposure of leaves, the uniform shape of plants, and the uniform size of fruits at a particular spacing. These characteristics make bush plants amenable to high density planting.

Physiological attributes of bush plants which contributed to high productivity were high mass transfer, facilitated by the larger phloem area and the proximity of sink organs to source leaves, a higher cumulative net assimilation rate (NAR) throughout development, a high crop growth rate (CGR), and high harvest index.

The attributes which limited productivity in the bush strain were the reduction in fruit size and quality at very high plant densities, the lower per cent dry matter of fruits produced at high plant densities, and the early senescence of leaves of bush plants during the later period of fruit development.

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